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- On page 444, fifth line from bottom, for " p. 29 " read " p. 458."
- On page 450, last line of note, for " p. 25 " read " p. 455."
- On page 455, fifteenth line from bottom, for "twenty-one legs" read "twenty-one pairs of legs."
- On page 457, three lines from top, for " *c. f.*" read " *cf.*"
- On page 467, sixth line from bottom, for "are" read "is."
- On page 484, tenth line from top, for "Strunstrip" read "Steenstrup."
- On page 485, sixteenth line from top, for "constructed" read "constricted."
- On page 487, last line (above footnote) dele the "1" after "(Sclater)."
- 
- On page 474, eighteenth line from top, for "higher" read "lighter."
- On page 476, ninth line from top, for "fig. 27" read "fig. 29."
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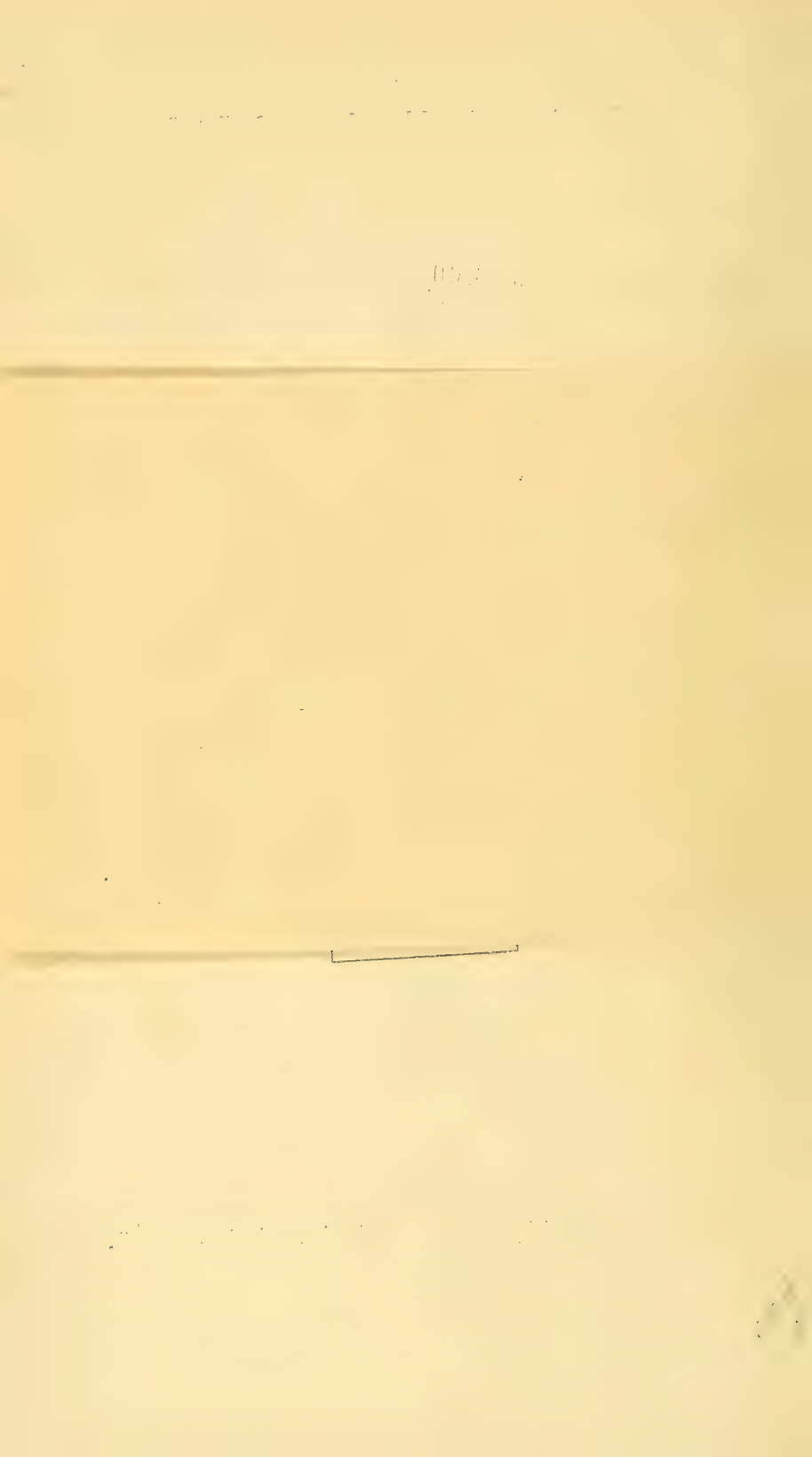
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- On page 439, twelfth line from bottom, for "Pl. I" read "Pl. XXXIV."
- On page 441, fourteenth line from top, for "Pl. I" read "Pl. XXXIV."
- On page 448, fifth line from bottom, for "6 mm." read ".6 mm."
- On page 455, ninth and tenth lines from bottom, for "legs" read "pairs of legs."
- On page 464, eleventh line from bottom, for "discernable" read "discernible."
- On page 467, ninth line from bottom, for "twenty-nine and" read "twenty-nine pairs and." On the next line, for "legs" read "pairs of legs."
- On page 468, sixth and tenth lines from top, for "legs" read "pairs of legs."
- On page 468, twelfth line from top, for "twenty-three" read "thirty-three."
- On page 468, tenth, eighth, and sixth lines from bottom, and on the last line, for "legs" read "pairs of legs."
- On page 471, seventeenth, nineteenth, and twenty-first lines from top, for "legs" read "pairs of legs."
- On page 474, eighteenth line from top, for "higher" read "lighter."
- On page 476, ninth line from top, for "fig. 27" read "fig. 29."
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## The Anatomy of the Madreporaria: III.

By

**G. Herbert Fowler, B.A.Oxon., Ph.D.,**

Berkeley Fellow of the Owens College, Manchester.

---

With Plates I, II.

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THE present memoir deals with the anatomy of *Turbinaria* (p. 1), a colonial Perforate coral; of *Lophohelia* (p. 6), an Imperforate form, colonial but with separate calyces; and of the two aberrant Imperforate genera, *Seriatopora* (p. 10) and *Pocillopora* (p. 13), in which the calyces are merged in cœnenchyme. To these descriptions is appended a note on the skeleton of *Flabellum*.

The most important facts now described for the first time are—1. The absence of directive mesenteries in *Lophohelia*, which thus differs from all Hexactiniæ hitherto described. 2. The retraction of the tentacles of *Seriatopora* by introversion, of which no other instance is known among the Madreporaria. 3. The presence of centres of calcification in the theca.

As in previous memoirs (2. 3), I have endeavoured to let the figures speak for themselves rather than to give detailed descriptions of structure.

### *TURBINARIA*, sp. (figs. 1—3).

For the opportunity of investigating this form, as in previous instances, I am indebted to the liberality of my teacher, Professor H. N. Moseley, who procured the material during the voyage of H.M.S. "Challenger."

i. *Corallum*.—The colony is crateriform or goblet shaped,

the calyces of the polyps being placed on the inner face and on the brim of the goblet. The cœnenchyme is porous, in the manner characteristic of the Perforata, but the echinulations are not arranged in costæ with the regularity observable in some genera, except on the actual thecæ of the polyps. The latter project outwards from the cœnenchyme only abaxially, i. e. inwards towards the centre of the goblet, the axial half being almost level with the general surface. Specimens of the coralla of this genus are not uncommon in museums; a detailed description and figures are therefore unnecessary, and may be found in the works of the authors appended below (p. 6).

Owing to the small amount of the material at command, none could be spared for the determination of the species. It appeared, however, to belong to the type of *T. mesenterina*.

The septa, in fully-grown polyps of this particular species, vary much in number, but are generally from seventeen to twenty-two; they are entocœlic only. It is worthy of remark that the number of septa appears to bear no relation to any multiple of six, nor can any division into orders be effected, since all are approximately of the same length. A loose and incomplete columella, occurring deep down in the calices, appears to be referable to fusion of the septa.

Part of a transverse section through the corallum (made according to the balsam and ether method introduced by von Koch) is represented in fig. 1, showing sections through at least five polyp cavities. Of these one, *a*, is cut obliquely, owing to the sharp angle at which the polyp cavities are inclined to the general axis of the colony; of the others, which are cut through at varying distances from their orifices, that lettered *b* is a nearly transverse section, of a typical character, exhibiting eighteen septa; while the three others, *c*, show the reduction of the septa in the deeper parts of the cavities. The upper part of the figure represents the abaxial, the lower the axial, surface of the crateriform colony. The echinulations and canal system are also well shown in this section.

ii. *Anatomy*.—The whole colony, both inside and outside of the goblet, is clothed with an external body wall of ectoderm,

mesoglœa,<sup>1</sup> and endoderm, exactly as has been described in Stylophora (7), Madrepora (3), &c.; its continuity is only broken by the mouth orifices of the polyps.

What the exact relation of this body wall to the tissues actually apposed to the theca may be, i. e. whether it agrees with the undoubted relations described in *Astroides* embryo (8), in *Dendrophyllia* (5), and *Rhodopsammia* (2), or with the apparently equally accurate relations recorded for *Stylophora* (7) and *Madrepora* (3), is exceedingly difficult to determine. In my specimens, both of *Madrepora* and *Turbinaria*, the contraction produced by preservation in alcohol has forced the body wall so tightly upon the echinulations that they project in many cases through it. Again, in *Heteropsammia multilobata*, a form as closely allied to *Rhodopsammia* as one with cœnenchyme can be to one devoid of it, the relations appear to be identical with those in *Madrepora* and *Stylophora*, and such as I have here (fig. 2) drawn for *Turbinaria*. If we are justified in crediting the appearance of the tissues in *Stylophora*, *Madrepora*, and *Turbinaria*, which implies that the body wall is supported upon the echinulations (fig. 2), it is not perhaps too much to infer that these relations are of secondary significance, and have arisen contemporaneously with the development of cœnenchyme, for the support of the external body wall, owing to the inadequacy of the peripheral sections of the mesenteries to effect this support elsewhere than immediately round the theca (where this is exerted from the cœnenchyme). In other words, the mesenteries are necessarily confined to the polyp cavity, and their peripheral sections to the small part of it which is cut off (?) from the rest by the upward growth of the theca; while therefore they are amply sufficient for the support of the body wall in a form with separate free calicles (e. g. *Rhodopsammia*), they could not extend over the cœnenchyme of a form with fused or sunken calicles (e. g. *Heteropsammia*

<sup>1</sup> The substitution of this word for the misleading "mesoderm" we owe to Bourne (1).

multilobata), which is, by its very nature, outside of, and in a manner independent of, the polyp cavities.

Of the more primitive (?) condition, *Astroides embryo* (8), *Rhodopsammia* (2), *Dendrophyllia* (5), and *Fungia* (1) stand as admitted examples among the *Perforata*; *Cladocora* (4), and *Caryophyllia* (6) among the *Imperforata*, all being forms with free calyces; while of the secondary condition, *Madrepora* (4), *Heteropsammia multilobata* (which I hope to describe in a future memoir), *Turbinaria* among the *Perforata*, and *Stylophora* (7), *Seriatopora* and *Pocillopora* (described below) among the *Imperforata*, are the recorded instances, all possessing well-developed *cœnenchyme*.

In a minor point only do my observations differ from those of von Koch (7), viz. that he figures no *mesoglœa* between the echinulations and the ectoderm; in other words, according to his figure the persistent ectoderm of the body wall is at those points continuous with the calicoblast layer (fig. 5). The reason which leads me to believe in the existence of a *mesoglœa lamina* between calicoblasts and external ectoderm, is that at the points where through shrinkage the echinulations have pierced the external body wall, they have carried with them this *mesoglœa*, which in sections of decalcified specimens preserves accurately their outline, projecting far beyond the shrunken ectoderm.

Between this external body wall and the corallum lies the system of approximately longitudinal canals with transverse commissures; in other words, the space between the body wall and the theca is broken up into canals by the points of contact. These canals communicate, as is usual in *Perforata*, with the canals which permeate the corallum and run also into the polyp cavities.

The polyps are built on the normal Actinian type. As the calices are placed only on the inner side and on the lip of the crateriform colony, an easy identification of bilaterality is thus afforded, the dividing plane being a radius directed to the centre of the goblet. Approximately at the ends of this dividing plane are placed the axial and abaxial



pairs of "directive" mesenteries, distinguished by the arrangement of retractor muscles on their ectocœlic faces. The polyps are not, however, rigidly bisymmetrical, inasmuch as the pairs of mesenteries lying right and left of the dividing plane are not equal in number.

The total number of pairs of mesenteries is not constant, but does not appear to depend upon the size (age) of the particular polyp. It varies generally from 17 to 22. The asymmetry of the polyps can best be seen in a tabular form :

	A	B	C
Number of pairs of mesenteries .	17	20	22
Number on right side of "directives"	7	10	9
Number on left side of "directives"	8	8	11

The three polyps here quoted were within a few millimetres of each other, and all were nearly of the same size.

The number of pairs of mesenteries is of course the same as that of the septa, the latter being entocœlic only, though a misleading appearance of ectocœlic septa is produced by the fact that some pairs of mesenteries die out after a very short course, while their septa are still recognisable at a much greater depth in the polyp cavity. The mesenteries with a longer course are in all respects perfectly normal, and in my specimens bore huge ova, the structure and relations of which call for no special comment (fig. 3.) The length or shortness of the mesenteries appears dependent on no particular system, such as has been observed in some other forms (3).

The tentacles are probably entocœlic only, but are so retracted as to render the point somewhat obscure. In this condition they are covered by a ring-fold formed of the indrawn margins of the disc, a method of protection common among the Actinaria.

The histology, though much spoilt by prolonged decalcification, agrees with that of the typical forms already described. The muscular pleats of the mesogloea of the mesenteries are only very slightly and irregularly developed, but entirely normal. Nematocysts are closely packed together in the



tentacles; they are not however, arranged in knobs or "batteries."

Zooxanthellæ are present abundantly in the canals exterior to the theca, in the tentacle cavities, and immediately under the mouth disc; elsewhere they are comparatively rare.

iii. Summary.—The following are the most important points elucidated:

1. The polyps are of the normal Actinian type, and are bilateral, but not rigidly bisymmetrical.

2. The septa and tentacles (?) are entocœlic only.

3. The number of septa present is inconstant, and bears no relation to any multiple of six.

4. The general body wall of the colony is supported upon the echinulations of the cœnenchyme; a condition which may be of secondary significance, acquired for the purpose of such support, contemporaneously with and in consequence of the development of cœnenchyme.

iv. Memoirs referring to the Genus:

MILNE-EDWARDS and HAIME, 'Hist. Nat. des Coralliaires,' iii, 164, pl. E i, figs. 1a, 1b.

KLUNZINGER, 'Korallthiere des Rothen Meeres,' ii, 50.

#### LOPHOHELIA PROLIFERA (figs. 4—8).

The material for a study of this form was entrusted to me by Professor E. Ray Lankester, who had dredged it off Lervik, Stordoe, Norway, and whom I am glad to be able thus to thank for his generosity. Owing to the great density of its corallum, and the consequent damage to the tissues produced by prolonged decalcification in a strongly acid medium, the work has been long delayed. Part of the material had been placed directly in absolute alcohol; part was passed from corrosive sublimate through successive strengths of spirit to 90 per cent. alcohol. Both sets were in excellent preservation, but the latter method appeared to be preferable, as resulting in less shrinkage of the tissues.

i. Corallum.—Of all corals this is probably the most generally

familiar, and requires here no systematic description. The theca, which terminates the branches of the corallum, is solid, as in all such Imperforata. The septa, which are exsert above the lip of the theca, are both ectocœlic and entocœlic, but are only irregularly arranged in orders. In a polyp with forty-eight septa, for instance, of which twenty-four are ectocœlic, the remaining twenty-four entocœlic septa are probably divisible into six primaries, six secondaries, and twelve tertiaries; but, as they all are approximately of the same length, this division is founded more on analogy than on distinctive differences. The total number of septa, which probably varies with the age of the individual polyp, is not necessarily a multiple of six or twelve.

Transverse sections of the corallum show, as has been recorded for other forms, e. g. *Cladocora* (4), *Caryophyllia* (6), that a dark line, indicating its earliest formed part, runs down the centre of each septum, and may be termed a "centre of calcification." In addition to these lines, however, sections, so made that they shall just cut the extreme lip of the actual theca, exhibit other "centres of calcification" between the enlarged ends of the septa, i. e. they lie in the theca itself (fig. 4). In sections at a lower plane the centres of calcification in the theca and in the exocœlic septa are found to have run into a continuous dark line (fig. 5), which at a yet lower level is joined by those of the entocœlic septa. There are thus three separate centres of active coral secretion at three different levels.

From fig. 5 it is also obvious that by far the greatest thickness of the coral is laid down peripherally, i. e. by the calicoblasts of the extrathecal part of the polyp. About six-sevenths of the thickness of the theca is due to these calicoblasts, while the remaining seventh is formed by those internal to the theca.

ii. **Anatomy.**—In spite of the great length of the branch on which it is borne the polyp is often comparatively short, measuring from 5 mm. to 20 mm.

As will probably prove to be the case in all the Imperforata

with free calyces (cf. *Cladocora* (4), *Caryophyllia* (6), &c.), the polyp is so continued over the lip and outer side of the calyx as to form a covering for its exterior surface to a varying distance (the "Rand-platte" of v. Heider). In *Lophohelia* this continuation may extend for about 15 mm., or even more; often it measures much less, and in it the relations of the various body layers are such as have been already described in the forms referred to above; the part of the coelenteron enclosed in this "Rand-platte" is divided up into exocœlic and entocœlic spaces nearly corresponding to those inside the calyx by the peripheral lamellæ which were at a former time continuous with the more central mesenteries, but which have been mainly cut off from them by the gradual growth of the theca upwards, though the continuity is maintained above the lip (fig. 6). This explanation, due originally to Dr. von Koch, must undoubtedly apply to this and many other adult forms.

The general anatomical relations of the polyp, and its agreement with forms already described, are shown in the diagrammatic segment of a transverse section (fig. 6). The "Rand-platte," the mouth disc, tentacles, and stomatodæum are all in accordance with the normal type. The coelenteron of the living polyp is, as usual, lined by endoderm and mesogloea, apposed directly (except for scattered calicoblasts) to the corallum. At the point, however, where the living polyp ceases, its coelenteron is separated off from the cavity in the coral which it previously occupied by a plug of decaying (?) tissue, in which no cell-elements or organic structure are recognisable, except occasionally the remains of the mesogloea lamina of a mesentery. Into this the living tissues pass gradually.

The tentacles, which are both ectocœlic and entocœlic, i. e. one over every septum, are knobbed, each knob being such a battery of nematocysts as has been described in *Flabellum* (2), *Stephanotrochus* (11), &c.

The mesenteries which, like the septa, vary in number in different polyps, all bear retractor muscles on their entocœlic faces, i. e. there are no pairs of "directive" mesenteries

at the opposite ends of the long axis of the oval stomatodæum, thus differing from those of all other Hexactiniæ or Madreporaria yet described. The significance of this fact cannot, of course, yet be understood, as nothing correspondingly abnormal occurs in any other part of the polyp with which it might be correlated. As, however, the mechanical or other function of the directive mesenteries is itself not yet explained, the meaning of the variation from the common type is naturally not appreciable. The number of the pairs of mesenteries, like that of the septa, is not necessarily a multiple of six.

The only point in the histology that appears worthy of note is the great length of the calicoblasts, as compared with that of the other cell-elements. A group of them from the edge of a growing septum is represented in fig. 7. Still more marked is the great length of these cells in fig. 8, which represents a transverse section through the tissues at that point where the upward growth of the theca divides the mesenteries into a central portion within the calyx, and a peripheral portion outside of it. Here they measure as much as  $\cdot 054$  mm. The large plate of mesoglœa in the centre of the figure is merely that which immediately overlies the lip of the calyx, and is cut in a direction parallel to its flattened surfaces, while the section passes nearly at a right angle to the other tissues. The point here figured is such a "centre of calcification" in the theca as has been already referred to ( vide p. 7).

iii. Summary.—The most important facts thus obtained are—

1. The polyps agree with the normal Actinian type, except for the absence of "directive mesenteries." They possess a well-developed "Rand-platte."<sup>1</sup>

2. The septa and tentacles are both ectocœlic and entocœlic, the number of septa not being necessarily a multiple of six.

3. Three series of centres of calcification are recognisable in the skeleton, of which one lies in the theca itself, and the

<sup>1</sup> It is, perhaps, unnecessary to coin an equivalent for this till its morphological value is better understood.



other two at the summits of the ectocœlic and entocœlic septa respectively.

iv. *Memoirs referring to the Genus :*

MILNE-EDWARDS and HAIME, 'Hist. Nat. des Corall.,' iii, 116.

STUDER, Steinkorallen auf der Reise S. M. "Gazelle" gesammelt, Monatsb. Akad. Berlin, 1877, p. 631, pl. I, fig. 8.

MOSELEY, "Challenger" Rep. Zool., ii, 178, pls. VIII, IX.

SERIATOPORA SUBULATA (figs. 9—13).

For the material for the study of this coral and of Pocillopora I again owe my thanks to Professor H. N. Moseley, who has already investigated the general anatomy of both forms (10). As, however, no structural details have yet been figured, and these somewhat aberrant forms are of great interest, no apology is necessary for a second account of them. The specimens of Seriatopora were obtained by Mr. Gulliver from Zanzibar.

i. *Corallum*.—The characteristic feature of the skeleton which caused both Seriatopora and Pocillopora to be ranked in the now abandoned group of Tabulata is the presence of tabulæ, i. e. successive floors of coral, by which the living polyp shuts off its cœlenteron from the cavity it previously occupied, a condition the opposite to that described above in Lophohelia prolifera. The calyces are therefore nearly confined to the outermost part of the colony, and are not continued deeply into it, as was the case in Turbinaria. These shallow calyces project but slightly above the cœnenchyme, and at a very short distance below the orifice are divided into two halves by the fusion of the two larger septa. These two septa, the axial and the abaxial, are the only two that are developed to any extent, though traces of the other ten may be recognised in many cases (cf. the condition of Madrepora Durvillei (3)). When all are present there are six entocœlic and six ectocœlic. It is perhaps more accurate to speak of the calyx as divided into two halves by the fusion of these septa than to regard the two chambers thus formed as special pits for the reception of the two longer mesenteries (10), since



they are simply downward continuations of the conical cœlenteron, and mesenteries other than the two longer ones are sometimes attached to their sides. Other details of the skeletal structure do not especially bear on the anatomy of the polyps.

ii. **Anatomy.**—As was shown by Professor Moseley, *Seriatopora* is undoubtedly a Madreporarian, and is even more in accordance with the normal types than could be inferred without the aid of sections.

The whole of the colony is clothed in the customary body wall of ectoderm, mesoglœa, and endoderm (fig. 9), which is supported on the echinulations of the cœnenchyme (vide supra, p. 3). The space between body wall and theca is broken up by these spines into a superficial series of canals (figs. 9, 10, 13), which ramify over the cœnenchyme and place the polyp cavities in communication with each other, but do not, of course, extend into the corallum in the manner characteristic of the *Perforata*. The body wall is continuous with the mouth disc, and from the centre of the latter rises a slight hypostome, through which opens the stomatodæum. This latter is crucial in transverse section, the longer arms of the cross being in the dividing plane of bilaterality indicated by the axial and abaxial septa (fig. 10).

The tentacles, which are twelve in number, being both ectocœlic and entocœlic, are simple evaginations of the cœlenteron, tipped with a terminal swelling, which is a single "battery" of nematocysts (fig. 11). There is, I believe, no instance yet recorded of the occurrence among Madreporaria of the method of tentacular retraction which distinguishes *Seriatopora*, namely, that of introversion (figs. 12, 13), the tentacles being invaginated in such wise that the battery is still pointed upwards. In fig. 13 the ectocœlic tentacles are expanded, while the entocœlic are introverted, a condition not uncommon in my specimens. Probably owing to the minuteness of the polyp, no special muscular apparatus for effecting this retraction could be detected.

The mesenteries, which are twelve in number, are arranged

in pairs<sup>1</sup> on the normal type. In the diagram (fig. 9) they are numbered in the same manner as those of *Madrepora* (3); the two mesenteries marked 3 and 10 respectively are comparatively long, extending to the bottom of the polyp cavity, and possess the thickened edge known as a mesenterial filament; of the rest, those numbered 1, 5, 8, 12, though generally devoid of a "filamentar" thickening, are recognisable in transverse sections for some distance below the stomatodæum; while the others, 2, 4, 6, 7, 9, 11, are rudimentary, and are visible only in the highest sections. It is worthy of remark that the six rudimentary mesenteries last mentioned are those which in the one type of polyp of *Madrepora Durvillei*, are pierced by a special ectodermal canal, and which in the other type of polyp of the same species, and in all the polyps of *M. aspera*, are distinguished from the remaining six by a greater length and the possession of a filamentar thickening; in other words, of the total twelve mesenteries the six which in the one form are the best developed are in the other quite rudimentary.

The histology agrees with that of the normal types. I have found no trace of generative organs in my specimens.

iii. Summary.—The interesting points in *Seriatopora* are:

1. The polyps are Actinian in structure.
2. The septa when all are present, and the tentacles, are both ectocœlic and entocœlic.
3. The tentacles are retracted by introversion.
4. The body wall is supported upon the echinulations of the cœnenchyme.
5. Of the twelve mesenteries, six (and more especially two of these) are of some length, and six are rudimentary; but

<sup>1</sup> Professor Moseley (10) states that in *Seriatopora* and *Pocillopora* the mesenteries "are not disposed in pairs with regard to the septa;" and the remark reappears in a misleading form in Professor Martin Duncan's "Revision of the Madreporaria" ('Journ. Linn. Soc. Zool.,' vol. xviii), to the effect that "the genera differ from other Madreporaria in not having their mesenteries arranged in pairs." The original statement was correct because the possibility of ectocœlic septa in a coral had not been demonstrated.

those which here are well developed are, in the Madreporæ mentioned above, rudimentary, and vice versâ.

iv. *Memoirs referring to the Genus :*

MILNE-EDWARDS and HAIME, 'Hist. Nat. Corall.,' iii, p. 311, pl. F 4, fig. 3.

KLUNZINGER, 'Korallthiere des Rothen Meeres,' ii, 69, pls. vii, viii.

AGASSIZ, 'Nat. Hist. United States,' iv, p. 296, pl. 15, fig. 15.

*POCILLOPORA BREVICORNIS* (figs. 14, 15).

The anatomy of this species agrees so closely with that of *Seriatopora subulata* that only points of difference between the two need be quoted.

The corallum is, of course, different in its mode of growth, as upon this the distinction between the two genera is based, but this difference does not affect the anatomical relations of the polyps. The method of support of the external body wall is identical with that in *Seriatopora*; the tentacles agree in the two forms, though, as they are fairly well expanded in my specimens, it does not appear whether they are capable of introversion or not; the stomatodæum is less distinctly conical than in the cognate genus.

As regards the mesenteries, the only points of difference noticeable are, that in *Pocillopora* those denoted in the diagram (fig. 9) by the numbers 3, 10, are not proportionately so much longer than those marked 1, 5, 8, 12, and that a mesenterial filament may sometimes be detected on the four last mentioned; in other words, the tendency observed in both *Seriatopora* and *Madr. Durvillei* towards the exclusive assumption of function on the part of six mesenteries and towards a correlated retrogression (?) on the part of the other six, has not attained to such a pitch in *Pocillop.* (and *Madr. aspera*) as in the other two forms.

The statement of Professor Moseley (10), that "the mesenterial filaments are not enclosed in prolongations of the

chamber walls" is not justified by the examination of sections; the two longer and more developed mesenteries with their filaments, 3. 10, lie, as in *Seriatopora*, for their whole length in the coelenteron.

Apparently, any of the mesenteries may bear generative organs, and it is worthy of remark that the polyps are monœcious. The ovaries and testes, though surrounded by a thin capsule of mesogloea and endoderm, as in typical forms, do not lie, as is generally the case, in the plane of the mesenteries (cf. fig. 3), but project from their sides in a manner more characteristic of certain *Alcyonaria*, so that in transverse sections of the colony they frequently appear to lie free in the coelenteron. Two stages in the development of the spermatozoa are figured as well as the preservation of the material would allow (figs. 14, 15).

In both this and *Seriatopora* there was left, after decalcification, a residue in the position occupied by the corallum, which, though staining faintly both with hæmatoxylin and with borax carmine, showed no distinctly organic structure.

In transverse sections of the polyps it is just possible to detect, at the point of the insertion of the mesenteries in the corallum, structures similar to those described by Sclater (11) as calicoblasts. Their excessive minuteness in *Pocillopora* rendered an accurate investigation impossible, but they certainly appeared to me to be rather connected with the attachment of the mesentery to the corallum than with the secretion of coral.

MILNE-EDWARDS and HAIME, 'Hist. Nat. des Corall,' iii, p. 301, pl. f 4, figs. 1, 2.

AGASSIZ, 'Nat. Hist. United States,' iv, 295, pl. xv, 14.

KLUNZINGER, 'Korallthiere Roth. Meer.,' ii, 66, pls. vii, viii.

#### NOTE ON THE SKELETON OF FLABELLUM.

In his latest addition to the literature of the subject (9), the main part of which I do not propose at present to discuss, Dr. von Koch treats, amongst others, of the skeleton of *Flabellum*.



1. He states that the dark line of growth, visible in transverse sections of the calyx, which indicates the earliest formed part of the coral at that level, is in Flabellum placed peripherally (fig. 16), and consequently that the skeleton is laid down from without inwards.

2. Elsewhere in the same paper he infers, from his researches on the development of *Astroides calycularis* (8) that the epitheca of all corals, originally deposited outside the lateral body wall of the embryo, also increases in thickness on the inner side only.

3. Finally, we find that "diese Koralle bildet einen ganz eigenen Typus, wegen des gänzlichen Fehlens der Innen-platte. Die Aussen-platte<sup>1</sup> ist gut entwickelt . . . Die Homologisirung der Aussen-platte mit der Innen-platte (Theca) der vorhin beschriebenen Korallen wird aus der Struktur derselben als irrig erkannt."

The implied argument may thus be expressed in the syllogism :

1. The skeleton of Flabellum grows in thickness from without inwards.

2. An epitheca grows in thickness from without inwards.

3. Therefore the skeleton of Flabellum is an epitheca—an example of what is characterised by logicians as the fallacy of the undistributed middle term ("Medium non Distributum").

Dr. von Koch is no doubt correct in asserting that the calyx of Flabellum is laid down from without inwards ; but till clearer evidence be adduced to the contrary it is far simpler to regard it as a theca entirely homologous with the theca of typical Madreporaria (or at least with a part thereof), than to conceive that the epitheca, which we know elsewhere only as an inconstant and inconsiderable structure, should have replaced the solid theca, merely to achieve the same physiological end.

Nor is there anything in the structure of the corallum really inconsistent with the idea that it is a theca. The embryonic Flabellum patagonicum attaches itself to an Arenaceous

<sup>1</sup> I. e., Epitheca.



Foraminifer, or some similar body (v. Moseley, 'Rep. Chall. Zool.,' ii, Madrep., pl. xv, figs. 1, 2) ; but the adult is entirely free, and therefore more or less at the mercy of natural accidents, such as currents. Correspondingly with this condition, but unlike that of the attached forms (*Lophohelia*, *Caryophyllia*, &c.) it develops no "Rand-platte," (vide p. 8), but the polyp can be wholly retracted within the calyx (cf. (2) fig. 2). The absence of the "Rand-platte" implies almost necessarily the absence of extracalicular calicoblasts ; the calyx must therefore be deposited by those internal to the corallum. As a consequence of these facts, the calyx of *Flabellum*, if it be not an epitheca, would be homologous with that part of the theca of *Lophohelia*, &c., which lies internal to the dark line of growth mentioned above (p. 7) ; and a comparison of fig. 16 with figs. 4, 5, will show that there is no discordance between the two structures.

In both forms, as is generally the case, the regions due to separate centres of coral secretion are bounded by sutures ; and of these regions those marked T. (thecal), and S. (septal), in all three figures certainly appear to be respectively homologous. Even the way in which the dark line in *Lophohelia* curves inwards to the ectocœlic septum (owing to the fact that at the lip the latter does not project so far peripherally as an entocœlic septum) agrees with the involution of the septa in *Flabellum*. The fact that in fig. 5 the centre of calcification of the entocœlic septum projects outwards through the line of growth, is of course attributable to the pseudo-costæ occurring at the lip of the calicle of this species of *Lophohelia* which are produced by extra-calicular calicoblasts and are not therefore represented in *Flabellum*.

In fig. 17 is drawn a transverse section through a part of the pedicle, that is to say a section through the corallum of an embryo *Flabellum* measuring about 2.25 mm. in diameter and possessing six primary and six secondary septa. The relations indicated by the sutures are the same as in the former section. The successive laminæ showing the conversion of the embryonic calyx into a nearly solid pedicle are well marked.

In conclusion, I have to express my thanks to Professor Milnes Marshall for his assistance; and to the anonymous donor of the Berkeley Fellowships in the Owens College, whose generosity has enabled me to carry on my studies.

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## EXPLANATION OF PLATES I and II.

## Illustrating Mr. G. Herbert Fowler's Paper on "The Anatomy of the Madreporaria," III.

FIG. 1.—Transverse section through a small part of the crateriform colony of *Turbinaria* sp. (vide p. 2). *Ab.* Abaxial, inner, or ventral surface of the colony. *Ax.* Axial, outer, or dorsal surface of the colony. *a.* Oblique section through a polyp cavity. *b.* Transverse section of a polyp cavity near its orifice. *c—c.* Similar sections further from the orifices. (Camera lucida.)

FIG. 2.—Diagrammatic transverse section of a polyp of *Turbinaria* sp. (p. 3). In this and similar diagrams the ectoderm is represented by "blocked" black and white, the mesogloea by a dark line, and the endoderm by a light line, the calcareous skeleton being dotted. The thicker and contorted ectoderm at the upper part of the stomatodæum represents the taller cells, interspersed with plentiful nematocysts, occurring in the neighbourhood of the tentacles, i. e. mouth disc rather than stomatodæum. Twenty-two pairs of mesenteries occur in this polyp, of which eleven are on the right and nine on the left of the "directives." A bit of the external body wall is drawn to show its relations to the echinulations. *Ab.D.* Abaxial directives. *Ax.D.* Axial directives. *St.* Stomatodæum. *Ect.* Ectoderm. *Me.* Mesogloea. *En.* Endoderm. (Cam. luc.)

FIG. 3.—Transverse section of a mesentery of *Turbinaria* sp., bearing an ovum with nucleus, nucleolus, and nucleoleoli. The lengthening of the endoderm cells round the ovum is noticeable.

FIG. 4.—Transverse section of the calyx of *Lophohelia prolifera* near the lip (vide p. 7). The darker parts represent "centres of calcification," or the earliest deposited portions, which become enlarged into the regions marked respectively *T.* (thecal), or *S.* (septal), according to their origin. The regions are bounded by "sutures." *Ect. s.* Ectocœlic septa. *Ent. s.* Entocœlic septum.

FIG. 5.—Similar section of *Lophohelia prolifera* at some distance from the lip of the corallum. The "centres of calcification" of the ectocœlic septa and of the theca have run into one line, owing to the growth of the latter upwards to the former. Lettering as in Fig. 4.

FIG. 6.—Diagrammatic transverse section through a segment of *Lophohelia prolifera*. The septa are seen to stand in both ectocœlic and entocœlic spaces. The peripheral sections of these spaces and the peripheral lamellæ of the mesenteries, cut off by the upgrowth of the theca, are also apparent. Lettering as in Fig. 2.

FIG. 7.—Tissue from the growing edge of a septum of *Lophohelia*, obtained by a longitudinal section of the polyp. *cb.* Calicoblasts. *me.* Mesogloea. *en.* Endoderm.

FIG. 8.—Tissue surrounding a thecal centre of calcification, obtained by a transverse section of the polyp (vide p. 9), showing the separation of a mesentery into central and peripheral parts in process. *Cæl.* Intrathecal coelenteron. *Cæl'.* Extrathecal coelenteron. *M.* The central, and *M'* the peripheral part of the mesentery. Other letters as before. (Cam. luc.)

FIG. 9. Transverse diagrammatic section of a polyp of *Seriatopora subulata*. The mesenteries are numbered 1—12, in the same manner as the *Madrepore* before described (3). Letters as in Fig. 2. (This diagram is also good for *Pocillopora*.)

FIG. 10.—View of a polyp of *Seriatopora* from above. The clearer spaces in the body wall of the colony represent the positions of the echinulations on which the body wall is supported, they having been dissolved away by acid. Through the body wall are seen the pair of longer mesenteries, 3 and 10. (Cam. luc.)

FIG. 11. Longitudinal section of a partly expanded tentacle of *Seriatopora*, showing the single battery of nematocysts at the tip, interspersed with a few deeply staining gland-cells.

FIG. 12.—Diagram of a longitudinal section of an introverted tentacle of *Seriatopora*. *B.* The battery of nematocysts, pointed upwards.

FIG. 13.—Diagram of an ideal longitudinal section through a polyp of *Seriatopora*, along the line *a—a* in Fig. 9. Of the six tentacles, three are expanded and three are introverted, one of the latter being cut longitudinally. Of the mesenteries, that on the right of the fig. (10) is one of the two longest; that on the left (5) is much shorter; while 6 and 7 are rudimentary, and do not reach as far as the end of the stomatodæum. The cavity is divided into two halves by fusion of the axial and abaxial into one median septum.

FIG. 14.—Early stage in the development of spermatozoa in *Pocillopora*.

FIG. 15.—Later stage of the same. The testis is surrounded on all sides by endoderm, owing to the projection of the capsule outwards from the plane of the mesentery (vide p. 14).

FIG. 16.—Transverse section through the calyx of *Flabellum* (vide p. 16). The numbers ii, iii, iv, indicate the orders to which the septa respectively belong. Other letters as Fig. 4.

FIG. 17.—Transverse section through part of the pedicle of *Flabellum*, showing the conversion of the embryonic theca into a nearly solid pedicle. i, ii. Primary and secondary septa.





On the Anatomy of *Mussa* and *Euphyllia*,  
and the Morphology of the Madreporarian  
Skeleton.

By

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With Plates III and IV.

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THE following paper contains a description of the anatomy of two genera of *Madreporaria* *aporosa*, *Mussa* and *Euphyllia*, concluding with a general account of the morphology of the Madreporarian skeleton in the light of the most recent researches on the group. My thanks are due to Professor Moseley, who kindly gave me the specimens of *Euphyllia* with which I worked, and assisted me with his advice; to Mr. W. Hatchett Jackson, whom I frequently consulted on the more general morphological questions contained in the latter part of this paper; and to Dr. G. H. Fowler, who kindly lent me for reference proofs of his latest paper on the *Madreporaria* before it had appeared in public print.

*Mussa* (figs. 1—5 and fig. 17).—For the investigation of this form I had a number of specimens of *Mussa corymbosa*, collected by me during my visit to Diego Garcia (S. lat.  $7^{\circ} 13'$ , E. long.  $72^{\circ} 23'$ ). These corals grow in large quantities in the more sheltered parts of the lagoon in shallow water. The specimens I collected were covered by three to five feet of water at low spring tides. The colonies are *cæspitose*, the aggregate of the polypes forming what is apparently a very solid mass,

which proves, however, to be exceedingly fragile, since the polypes are borne on long calcareous stems, which readily break off at their bases. Mr. A. Dendy, of the British Museum of Natural History, has kindly identified the species for me, which is described by Milne-Edwards and Haime ('Nat. Hist. des Coralliaires,' tom. ii, p. 333) as follows:

"Corallites sometimes entirely free, sometimes united in small series of three or four. Spines on the theca widely separate from one another. Costæ well defined in the region of the calyces only. Columella rudimentary; four cycles of septa, the principal septa subequal, often decurved towards the inner margins, which are scarcely at all dentate; above they bear three stout, diverging spines. The smaller septa have tolerably regular, short, and pointed teeth. The polypes are, according to Ehrenberg, of a pale brown, with a golden-yellow disc. The margin is covered with bursiform papillæ which surround a small number of short digitate tentacles."

To this I have to add that the number of septa is very inconstant, and bears no relation to a multiple of six. In one calyx I counted thirty-two septa, in another forty-six, in a third (fig. 3) forty. In the last case twenty-four septa are of conspicuously larger size than the remainder, but do not show any characters which enable them to be classed as primaries, secondaries, &c. Their shape is accurately shown in section in fig. 3; the broader peripheral part can be distinguished from the more slender central portion, and the processes connecting the peripheral ends are easily seen. They are extremely exsert, standing as much as 9 mm. above the lip of the calyx. In the majority of cases one or sometimes two smaller septa are found between each pair of larger septa; these are thinner and smaller, and of approximately the same breadth throughout their course. Finding it impossible to separate the septa into regular systems, I shall refer to the first as the principal, the second as the secondary septa. The theca is formed by fusion of the peripheral ends of the septa (see fig. 2), and is only consolidated at some distance below the edge of the calyx. The upper part of the corallite is smooth and polished, corre-

sponding to the region that is covered externally by soft tissues. Below this the corallum is invested by a distinct coat of thin granular epitheca. The septa are united within the calyx by dissepiments, thin obliquely placed lamellæ of calcareous tissue placed at different heights in the interseptal loculi, and meeting towards the centre of the calyx (see fig. 4 *d*).

The colour of my specimens and the tentacles differ from Ehrenberg's account. The *Mussa* of Diego Garcia is of a dull brown colour, with olive-green disc and tentacles, the latter being numerous and moderately long. The polyps contract energetically on being handled, and I was unable to preserve any specimens with the tentacles expanded; indeed, all my specimens are so much contracted that the tentacles are no longer recognisable even in section. A view of a system of three polyps borne on a common stem is given in fig. 1, the drawing is taken from a specimen contracted in spirit, and is half the natural size.

Fig. 2 is a transverse section of a corallum of *Mussa* taken just below the lip of the calyx. In each septum may be distinguished dark centres of calcification, around which are seen a number of concentric, dark, and light lines of growth, marking successive additions of calcareous tissue. Evidence may also be seen of centrifugal growth of each septum, due to the deposition of calcareous matter on its peripheral extremity. The septa are seen to be joined together by wing-like outgrowths, which fuse to form a theca. At a lower level the theca would be seen to be consolidated by a continuation of the peripheral lamellæ of the septa over the intervening bridges of tissue, which thus externally cement the conjoined septa into a continuous whole.

Anatomy of the Polyp.—A glance at fig. 1 will show that the soft tissues of the polyp extend downwards for a considerable distance on the outside of the corallum. There is in fact a well developed "Randplatte," as it is called by German authors, and it contains extrathecal continuations of the exocœles and entocœles separated from one another by peri-

pheral continuations of the mesenteries, as has been described for other forms by von Koch, Fowler, and others. Fig. 4 shows that the "Randplatte" extends downwards considerably farther than do the soft tissues within the calyx. There can be no question that the "Randplatte" is a distinct structure in these forms.

As decalcification proceeds it becomes obvious that the corallum lies wholly external to the polyp, being, as it were, dovetailed into it from below; or, to use another illustration, the polyp appears to be drawn over the corallum much as a glove is drawn over the hand. After decalcification, the intracalicular soft tissues appear to be divided up into wedges by the spaces previously occupied by the septa.

Examination of the internal structure shows that it is of the normal Actinian type except in one important point, there are no directive mesenteries, the longitudinal muscles of each pair of mesenteries being placed vis à vis. This character, which has already been discovered by Fowler in *Lophohelia*, is also characteristic of *Euphyllia*, as will be seen later on. The arrangement of the mesenteries and their relations to the septa are shown in fig. 5. Each pair of mesenteries embraces a septum, all the septa are entocœlic, no septa occurring between pairs of mesenteries. The mesenteries embracing the principal septa are all inserted on the stomodæum, which is of moderate length; the mesenteries embracing the secondary septa are free throughout their extent. All the mesenteries bear well-developed filaments on their free edges, and below the stomodæum their edges are drawn out in long, sinuous, ribbon-shaped prolongations, around the whole edge of which the filament is continued, the whole structure being coiled up to one side of the mesentery in an exocœlic or entocœlic space. To such coiled filaments I erroneously gave the name of *Acontia* in my paper on *Fungia*, but I have since satisfied myself that they differ essentially from *Acontia* as defined by Gosse and the Hertwigs. Since the septa are all entocœlic the number of pairs of mesenteries is the same as the number of septa, and therefore not necessarily a multiple of six.



The tentacles were so completely retracted in my specimens that I could not determine anything about them. In some longitudinal sections there are infoldings on the surface of the peristome, such as are represented in fig. 4, but I could not say with any certainty whether these are tentacles or not. The ectoderm lining the involutions does not differ from that of the rest of the body surface.

Histology.—This does not differ from the normal Actinian type. The ectoderm is of the ordinary character, and contains numerous nematocysts .002 mm. in length when inverted.

The calicoblasts in most situations agree with the form described in *Fungia*, and the majority of cases, namely, rounded or polygonal, soft-looking granular cells, which do not stain easily, possessing nuclei which stain but slightly in borax carmine. They occur everywhere, in a scattered condition or forming a distinct layer, between the mesoglœa and the corallum. The calicoblasts which clothe the uppermost and peripheral parts of the septa are of a different character, being drawn out into very long, narrow, columnar cells, just like those described by Fowler for *Lophohelia*; and it will be observed that they correspond very closely in position to the similar cells in that form. In both cases they are found at the seat of the greatest activity of coral secretion. In several of my preparations I found pyramidal or oval cells exhibiting a longitudinal or radial striation, which exactly resemble those drawn by Sclater for *Stephanotrochus* and von Heider for *Astroides*, and described by them as calicoblasts. I have no hesitation in saying that in *Mussa* they are not calicoblasts, since they differ entirely from the cells above described, which from their position are undoubtedly calicoblasts, and they are never found in the regions of coral secretion. On the contrary, in my specimens they are always and only associated with the mesoglœa of the mesenteries. Fowler at the close of his account of *Pocillopora* describes similar structures, and considers that they are rather connected with the attachment of the mesentery to the corallum than with the secretion of coral. My observations fully confirm his views. It is important to bear in mind that these



structures are not calicoblasts, since von Heider, from his observations on them in *Astroides*, has recently inferred that the calcareous tissue is deposited in the form of crystals within the calicoblasts, just as the spicules are formed within the substance of the skeletogenous cells in *Alcyonaria* and calcareous sponges, and that the radial striation seen in these pretended calicoblasts is due to the presence of minute crystal of carbonate of lime. Now we know that animal tissues on the verge of calcification are extremely resistant to the action of acids, but in this case the crystalline form being assumed, that stage would have been passed, and the crystals, if they were such, would have been readily soluble in acids. Yet the acids which dissolved the whole coralla of the specimens which von Heider examined did not suffice to dissolve the minute crystals also. It might have been inferred, one would have thought, that whatever the striation was due to, it was not due to the presence of crystals of calcium carbonate. There is then nothing to disprove von Koch's statement that the calcareous tissue is elaborated by and secreted by the ectoderm (i. e. calicoblasts), and that the Madreporarian skeleton differs wholly in this respect from that of *Alcyonaria*.

The mesoglœa in *Mussa* is perfectly structureless; I failed to detect even a fibrillar arrangement in it, except were it is drawn out into pleats for the attachment of the longitudinal mesenterial muscles. In the upper part of the polyp, that part which occupies the spaces between the enormously exsert septa, the mesoglœa is enormously developed, giving a considerable amount of stiffness to the tissues in this region (fig. 4).

The endoderm is of the normal character, and is packed, as is usually the case in *Actiniaria*, with zooxanthellæ. The cells covering the mesenterial filaments are long and columnar, and contain many nematocysts of different kinds; the one kind small, similar to those found in the ectoderm, the other kind large, measuring .005 mm. in length when the thread is not ejected.

Ova were present in my specimens in the normal position, towards the lower extremity of the mesenteries, embedded in

the mesoglœa. They are of large size, measuring as much as .011 mm. across. They are only to be found on a few, and those invariably the shorter mesenteries; but they were not constant on these, and I am unable to say whether the shorter mesenteries alone are reproductive. As I found no traces of spermatozoa in the specimens which I examined it may be concluded that *Mussa* is monœcious.

*Euphyllia*.—The specimens of this genus were kindly supplied to me by Prof. Moseley, and form a part of the reef corals collected by H.M.S. "Challenger." The corallum is described by Quelch in the 'Challenger Reports,' vol. xvi, p. 74, as *Euphyllia glabrescens*. The description of the species by Milne-Edwards and Haime is as follows:—"Corallites sometimes unite in small series of three or four, but ordinarily separating early. Theca covered with closely set and extremely fine grains. Costæ thin, rising slightly near the edges of the calicle, and subcristiform. Calices with irregular boundaries, narrow, and very deep fossa. Septa very irregularly arranged in orders, scarcely exsert, very thin, moderately close together, their faces very finely granular, and presenting parallel striæ. Greatest width of the calices 2 centimetres; the diameter of the corallites is somewhat smaller beneath the calices."

Quelch arranges the septa in five orders, but I found their number very inconstant, and could not make out more than three definite cycles, which are, however, arranged with considerable regularity. The septa of the first order are large, and reach in the deeper parts of their courses nearly to the centre of the calyx. Those of the second order are rather shorter, and alternate with those of the first, whilst the septa of the third order are very short and are only to be found in the upper part of the calyx; they occur in every loculus between a septum of the first and a septum of the second order. A transverse section across part of the calyx, including septa of all three orders, is given in fig. 7. The calcareous tissues are seen to be much thinner and more fragile than in *Mussa*, and the concentric lines of growth seen in the latter form are not present. The centres of calcification are present as con-

spicuous dark lines running down the centre of each septum. The primary and secondary septa are but slightly thickened towards the peripheral ends, the theca being mainly composed of the heads of the tertiary septa. Fig. 7 shows that in the upper part of the calyx the tertiary septa project from a stouter thecal piece, the two together forming a T, of which the thecal portion is the cross-piece. There are no sutures separating the septal from the thecal portion. Lower down in the calyx the tertiary septa die out altogether, but the cross-pieces, representing their thecal portions, remain, and then the section has precisely the appearance figured by Fowler in *Lophohelia*. From the relations which obtain in *Euphyllia* I am not disposed to think that the intercalated pieces figured by him are essentially thecal structures sharply distinguishable from septa.

The structure of the dissepiments is quite similar to that of *Mussa*.

The specimens with which I worked were killed with the tentacles fully expanded, but they were unfortunately too much damaged to admit of a careful study. The tentacles are numerous, short, and apparently correspond in number to the septa, i. e. they are all entocœlic, as is the case with the latter.

A well-developed "Randplatte" is present as in *Mussa*, extending down the outside of the corallum for a distance of 1.5 centimetres. The structure and relations of the "Randplatte" are the same as those in *Mussa*, and do not require a detailed description, the only difference of importance is that whereas the longitudinal muscles are generally absent on the extrathecal portions of the mesenteries, they are present, although in a rudimentary form, in *Euphyllia*.

The appearance of the polyp on decalcification is quite similar to that of *Mussa*, and affords ocular demonstration of the fact that the corallum is wholly external to the polyp. The internal anatomy of the polyp is of the highest interest. I have not had the time to make so thorough an examination of its peculiarities as I should have wished, but hope to give a

fuller account of them in a future communication. At present I will confine myself to a description of what I have seen.

There are no directive mesenteries, *Euphyllia* agreeing in this respect with *Lophohelia* and *Mussa*. Their absence is a striking and important fact, adding as it does another type of mesenterial arrangement to those we know already. We have the normal Actinian arrangement, giving a bilateral symmetry along the long axis of the stomodæum, the Edwardsian and Alcyonarian arrangements in which the bilateral symmetry is marked equally well, but in a different manner. The arrangement in *Zoanthus* is clearly nothing more than a modification of the Actinian type, and the arrangement in *Cerianthus* is probably connected with an atrophy of the longitudinal muscles in the same type. All these forms show a bilateral symmetry; *Mussa*, *Lophohelia*, and *Euphyllia* alone are perfectly radial. This may either be a primitive condition or may be connected with fissiparity, for it is impossible to conceive how two polypes can be derived by fissiparity from one with directives, and yet the arrangement of directives be carried over into the daughter polyps, especially when an examination of an *Astræid* colony reveals the fact that the calices are constricted in their centres at right angles to their long axes, and the long axes of resulting calices may either be continuations of the long axis of the original calyx, from which they were derived, or may be set at right angles or any other angle to it. To state shortly the extraordinary features in the remainder of the anatomy, the stomodæum is very long, reaches nearly to the bottom of the polyp, and is converted into a ramifying and inosculating system of canals; it functions as the chief digestive cavity of the polyp. The endoderm is greatly vacuolated, and converted into a reticulated tissue filling up the cœlenteron, in the meshes of which are numerous nematocysts and symbiotic algæ. Mesenterial filaments are feebly developed on the primary and secondary mesenteries, which are attached throughout the greater part of their course to the stomodæum, and do not reach a great development on the tertiary mesenteries, which are free for the greater part of their course.



These peculiar modifications are shown in fig. 8. The histological details have been greatly simplified, but the outlines are correctly drawn with a camera lucida. The reticular endoderm *en'*, is seen filling up all the spaces corresponding to the cœlenteron. The stomodæal canals are shown at *st. c.* These canals are lined throughout by an epithelium exactly resembling that of the ectoderm on the free surfaces of the body, but staining rather more deeply in borax carmine. Great numbers of nematocysts are embedded in this epithelium, and may be seen in all stages of development. Fig. 9 is an unripe nematocyst, and corresponds with the stages drawn by Möbius in his account of the development of these structures. (Möbius, 'Ueber den Bau, den Mechanismus und die Entwicklung der Nesselkapseln,' Hamburg, 1866, Taf. ii, figs. 22 and 23). The ripe nematocyst, with its axial body ejected, is shown in fig. 10, and in fig. 11 it is drawn with the thread ejected, but not the axial body. The thread bears a peculiar armature at its extremity. The stomodæum below the mouth is a simple tube, but at a short distance lower it is produced into a number of horns running out towards the attachments of the mesenteries; at a lower level these horns are seen to have anastomosed with one another in such a manner that the stomodæum is converted into a highly complicated system of canals occupying the centre of the calyx. This is shown in section in fig. 8. At a lower level the stomodæum again becomes more simple, and finally ends in a simple, much compressed tube with a narrow lumen. I was unable to determine to my satisfaction whether the stomodæum opens below into the axial cavity, or whether it is completely closed. I am inclined to think that it opens by a very narrow passage. As the stomodæum reaches nearly to the bottom of the polyp cavity, the axial cavity below it is very small, and such as it is, it is entirely filled up with mesenterial filaments. The stomodæal canals contained numerous fragments of vegetable matter, apparently pieces of leaves. The presence of vegetable food in these canals is interesting, firstly, because I believe it is the only recorded instance of a coral feeding on a vegetable diet;



secondly, because it shows that this enormously and peculiarly developed stomodæum is digestive in function, which might, indeed, have been inferred from its extent, and from the almost complete absence of a cœlenteron as a cavity.

The mesoglœa is a thin but perfectly distinct, structureless lamina, everywhere separating the ectoderm from the endoderm. The endoderm cells lining the extrathecal parts of the cœlenteron are vacuolated, and do not fill up the cavities, but in the intrathecal parts of the polyp the endoderm cells are entirely converted into a parenchymatous tissue, filling up all such parts of the cœlenteron as are not occupied by mesenterial filaments. My specimens were not sufficiently well preserved to admit of my giving an account of the histology of this tissue. It is filled with nematocysts, one of which is represented in fig. 12, and may be seen to be of an entirely different character to those found in the ectoderm, being of smaller size and different shape. The axial tube is distinguishable, and the thread coiled in an oblique spiral within the capsule. I could not find any of these nematocysts with the thread ejected. Numerous zooxanthellæ also exist within the meshes of this tissue.

The muscles on the mesenteries are well developed, and exhibit the relations of the exocœles and entocœles. The septa are all entocœlic.

Ova are borne on the tertiary mesenteries and on them only. The ovaries are of large size and bulge out the mesenteries to such an extent that they nearly fill up the exocœles and entocœles in that region. They are always developed towards the peripheral ends of the mesenteries. Each ovum is surrounded by a number of large granular masses the granules of which stain very deeply in borax carmine. At first I mistook these for testes, but from their relation to the ova and their resemblance to nutritive cells in *Pennaria Cavolinii* and *Tubularia mesembryanthemum*, I have no doubt that they are nutritive cells destined to be absorbed by the ovum (vide fig. 8, *ov.*). That one out of several primitive ova should develop into a mature ovum at the expense of the others has

long been known in Hydroids, but has not previously been described for the Anthozoa. The cells of the mesenterial filaments are vacuolated, but their boundaries are clearly recognisable.

The structure of *Euphyllia* as above described is without parallel in the *Madreporaria*, or indeed in the Anthozoa, the ramified digestive tract and parenchymatous tissue suggest a comparison with *Dendrocœle* planarians; but the comparison will not hold good for a moment when we consider that the alimentary tract of the latter is formed from hypoblast, whilst that of *Euphyllia*, formed by the stomodæum, is ectodermic.

Any attempt to explain such isolated phenomena as these must be peculiarly liable to error, but possibly the following explanation may throw some light on the peculiarities. The endoderm of *Euphyllia* as of most *Madreporaria* is filled with symbiotic algæ. These contribute an important share towards the nutrition of the polyp, and it is conceivable that the symbiotic nutrition, if one may express it so, became of such primary importance to the economy of the animal that the endoderm lost its original digestive function and became vacuolar in order to accommodate greater numbers of zooxanthellæ. A comparison between the vacuolated endoderm of *Euphyllia* and the extracapsular protoplasm of the *Radiolaria*, will explain my meaning. In both cases the vacuolation is probably connected with the presence of zooxanthellæ. The ectoderm is known to retain the power of amœboid digestion in many *Cœlenterata*, including *Actinia mesembryanthemum* and *Bunodes sabelloides* (Metschnikoff, 'Researches on the Intracellular Digestion of Invertebrates,' this Journal, new ser., xxiv, p. 93). There is nothing surprising then that at the same time that the endoderm became modified in connection with symbiosis, that the ectoderm of the stomodæum should have taken a more active part in alimentation, and that its surface should be greatly increased to meet the remaining necessities of the organism.

It has long been felt that a classification of *Madreporarian*

corals based on a study of the corallum alone is unsatisfactory, and that any attempt to remodel the old classifications should depend on a systematic study of the relations between the corallum and the polyp. Owing to the difficulty of obtaining material, and of dealing with it when obtained, the number of forms examined is as yet small, and the results of recent researches have not advanced us very far towards an improved classification. The most recent attempt to remodel the systematic treatment of the group is Professor Martin Duncan's "Revision of the Families and Genera of the Madreporaria," 'Linn. Soc. Journ.,' xviii, in which the older classifications are amended in some important particulars, several old families have been struck out or merged with other families, and the Fungidæ are raised to the rank of a group equal in value to the Perforata and Aporosa. But whilst all the definitions, by far the greater part of the classification, depend on the old distinctions in the characters of the corallum, scarcely any weight is given to the development and anatomy of the polyp. Although but little has been done even in working out the anatomy of adult forms, and although our knowledge of the development of the Madreporaria is miserably insufficient, we have sufficient information about the group to enable us to make certain generalizations about it.

The principal workers on Madreporaria have been de Lacaze Duthiers, Moseley, G. von Koch, von Heider, and Fowler, whose separate memoirs are referred to in the course of this paper. In all, the anatomy of some twenty forms has been worked out more or less completely, and the development of one species, *Astroides calycularis*, has been followed by two observers, H. de Lacaze Duthiers ('Arch. de Zool. exper. et. gen.,' ii, 1873, p. 269), and G. von Koch ('Mitth. der Zool. Stat.,' Neapel, 1882).

**Anatomy of the Polyp.**—In the majority of the forms examined the structure of the polyp, both in grosser anatomy and in histology, is essentially that of an *Actinia*. The mesenteries are arranged in pairs, and frequently if not usually in cycles of six pairs each. But recent observations have shown

that the number of mesenteries, and with them of the septa, is inconstant in several genera, and that a hexamerous arrangement of the parts is by no means an invariable rule, so that the name Hexactinia as applied to the group is extremely misleading. In most cases the mesenteries are marked out into pairs by the situation of their longitudinal muscles, which are so arranged that in all but two pairs these muscles are attached to that side only of a mesentery which is turned towards its fellow. At the two ends of the long axis of the stomodæum, however, this arrangement is reversed, and these two pairs of "directive" mesenteries have the muscles on their opposite faces. This arrangement, which is typical of the Actiniæ, is found in nearly all the Madreporaria hitherto examined; but the latest researches of Fowler and myself show that directive mesenteries are absent in *Lophohelia* among the Oculinidæ, and in *Mussa* and *Euphyllia* among the Astræidæ. Excepting for this peculiarity *Lophohelia* and *Mussa* do not differ from the Actinian type; but *Euphyllia* is modified in an extraordinary manner, as has been described in the first part of this paper, and need not be recapitulated here. The other forms in which there is any important deviation from the normal type are *Pocillopora*, *Seriatopora*, and *Madrepora Durvillei*.

The anatomy of *Seriatopora* and *Pocillopora* was first investigated by Professor Moseley (this Journal, new series, xxii, p. 391), and his results have since been confirmed by Fowler. In these forms the main deviation from the normal Actinian type consists in the fact that of the twelve mesenteries only two bear mesenterial filaments, and these two do not belong to the same pair, but are the dorsal mesenteries of the right and left infero-lateral pairs respectively. In correlation with the development of the filaments on these two mesenteries the intermesenterial chambers or entocœles of the pairs to which they belong project far deeper into the calyx than the remaining chambers in *Seriatopora*; but this feature is not so well marked in *Pocillopora*. If the mesenteries are numbered from left to right, beginning with the left ventral or abaxial



mesentery, Nos. 3 and 10 are those with filaments and are longer than any others; Nos. 1, 5, 8, and 12 are recognisable for some distance below the stomodæum, Nos. 2, 4, 6, 7, 9, 11 are very short and rudimentary. In *Pocillopora* the difference in size between 3 and 10 and the other longer mesenteries, 1, 5, 8, 12, is not so marked as in *Seriatopora*, and the last named sometimes have rudimentary filaments. In both forms the polyps show a well-marked bilateral symmetry with regard to the dorsoventral axis, and in both there is a system of superficial radiating canals by which the cavities of adjacent polypes are put into communication with one another.

In *Madrepora Durvillei*, according to Fowler (this Journal, new ser., xxvii, pl. i), there is a well-marked dimorphism in the polyps composing a colony. In the one form of polyp there are twelve simple mesenteries, of which six have a long course and a better developed filament than the remainder, and of these two are longer than the others. In the second form of polyp are also twelve mesenteries, which in the higher parts of the polyp are perfectly normal, but at the lower end of the stomodæum six of them become modified, in all cases the same six, namely, the 2nd, 4th, 6th, 7th, 9th, and 11th, using the same method of counting as in *Seriatopora*. The modification consists in the greatly increased size and vacuolation of the endoderm cells of the mesentery, and in the presence of a canal lined by endoderm, which runs right through its centre and is bent sharply upon itself. For a description of the course of this canal and its relations to the polyp cavity, Fowler's memoir should be consulted. Only the modified mesenteries bear filaments, and of them two, viz. four and nine, are longer than the others. It is important to observe that the modified mesenteries of the second type of polyp correspond with the longer mesenteries of the first type, and that the longest mesenteries of all occupy the same positions in both cases.

In both *Seriatopora* and *Madrepora Durvillei* the two longest mesenteries alone bear gonads.

The differentiation of certain mesenteries in *Madrepora* and *Seriatopora*, and the specialisation in both cases of two mesen-



teries on opposite sides of the polyp for reproductive purposes, suggests a close affinity between the two forms; but there is this difference between them, that whereas the reproductive mesenteries in *Madrepora Durvillei* are 4 and 9, those in *Seriatopora* are 3 and 10, whilst the short mesenteries of the former correspond to the long mesenteries of the latter, and vice versâ. There are, however, other similarities in structure which ally the Pocilloporidæ with the Madreporinæ, although they are usually classed far apart, as *Aporosa* and *Perforata* respectively. In *Madrepora aspera* and *M. variabilis* the differentiation of the mesenteries does not appear to have advanced so far as in *M. Durvillei*. In the first named, according to Fowler, filaments are present on the abaxial directive mesenteries as well as on the same six as in *M. Durvillei*, the remaining mesenteries being devoid of filaments. Von Koch does not give any account of these structures in *M. variabilis*.

The Corallum.—In dealing with the hard tissues of Madreporarian corals I shall try to point out that there are only three (or possibly four) distinct structures in the corallum, viz. the septa, the theca, and the epitheca (and perhaps the basal plate). The columnella, the pali, the costae, the dissepiments, synapticula, exotheca, and peritheca may all be traced to modifications of the first named, and useful as they may be for the determination of genera and species, they have no morphological value. Associated with these names is the view that some of these structures differ fundamentally from the others; some were considered by Milne-Edwards and Haime to be of dermic origin, others to be of epithelial origin, whereas, as we shall see in the sequel, all the hard parts are of essentially similar origin.

The first point of interest connected with the corallum is to determine from which layer of the polyp it is derived, from the ectoderm, endoderm, or as a calcification of the mesogloea.

Milne-Edwards and Haime, in their classical work on corals, stated that the calcareous tissue was deposited in a layer which they called the dermis, which they defined as one of the

deeper layers of the ectoderm. This view, which for a long time held ground, was disputed by de Lacaze Duthiers, who states in his paper on the development of *Astroides calycularis*, that the calcareous tissue first makes its appearance in the endoderm<sup>1</sup> ('Arch. de Zool. Expér. et Gen.,' ii, 1873, p. 269). But since he did not recognise the existence of a third structureless layer—the mesoglœa—between the ectoderm and endoderm, and since his observations were not made by means of sections, de Lacaze Duthier's statements on this head are somewhat perplexing. It seems clear, however, that he considered the calcareous tissue to be deposited in the situation which further researches showed to be occupied by the mesoglœa, and it was from this layer that the corallum was thought to be formed by succeeding writers on the subject for some years.

The more exact relations of the corallum to the polyp have been chiefly worked out by G. von Koch, to whose works complete references will be found in my own and Fowler's papers on corals in this Journal.

From his observations on the development of *Astroides calycularis*, von Koch established the fact that the corallum is a product of the ectoderm, secreted by it, and makes its first appearance between the basal ectoderm and the surface to which the young *Astroides* is attached. His method of observation is at once ingenious and convincing. Pieces of cork were floated in the aquarium, to which free swimming larvæ soon attached themselves. As soon as it was apparent that a deposit of calcareous matter was being formed the embryos were killed in situ, and sections were cut through them and

<sup>1</sup> Fowler is in error in attributing to de Lacaze Duthiers the statement that the corallum is formed externally to the polyp. It is true that the figure to which he refers (fig. 27 of the memoir above quoted) fully bears the interpretation which he has given to it, but de Lacaze Duthiers' own words show that he took a very different view of the matter: "C'est au milieu, et dans l'épaisseur de cette couche interne, toujours plus épaisse dans le milieu et au bas des loges que se montrent les premiers nodules calcaires," and elsewhere he expressly defines what he means by the "couche interne;" it is the endoderm.

the cork to which they were attached. A diagrammatic drawing of a section made in this way, tangential to the surface of the polyp, is given in fig. 13; it is slightly modified from von Koch's original drawing for the sake of greater clearness.

Previous to von Koch's researches on *Astroides*, von Heider ('Sitz. der Kais. Akad. in Wien,' lxxxiv, 1881) had shown that in *Cladocora* there exists everywhere between the structureless mesogloea and the corallum a layer of rounded cells, which apparently have the function of secreting the coral substance; to these cells von Heider gave the appropriate name of calicoblasts, and considered them to be a product of the "mesoderm" (mesogloea), the layer from which he supposed the corallum to be derived. It is clear, however, from von Koch's researches, that the layer of calicoblasts is nothing more than the persistent ectoderm which secretes the corallum, and lies everywhere between it and the mesogloea. Unfortunately we are not acquainted with the development of any Madreporarian other than *Astroides*, but since calicoblasts have been found in all corals recently examined, we may assert with certainty that the corallum is a product of the ectoderm and is always external to the polyp.

In describing the formation of the theca, the septa, and the costae, the statements of de Lacaze Duthiers and von Koch differ widely from one another. The former states distinctly that the theca appears independently of the septa, the latter arising as twelve radiating rods, bifurcated at their peripheral extremities. As far as the number and shape of the rudiments of the septa are concerned, von Koch's statements are in accordance with those of de Lacaze Duthiers, but he gives a very different account of the formation of the theca. The skeleton, he says, first appears as a ring-shaped basal plate, incomplete in its central portion, this plate always making its appearance between the basal ectoderm and the surface to which the larva is attached. It is composed of an aggregation of small spherical nodules, each of which is made up of rhomboid calcareous crystals grouped in concentric layers. As growth proceeds the

basal plate becomes consolidated, and its central vacuity filled up. No doubt it was the earliest formed ring-shaped part of the basal plate which de Lacaze Duthiers took for the theca. The first signs of septa are twelve radially disposed ridges of the basal endoderm, which soon project upwards into the cavity of the polyp as a series of folds, the mesogloea and ectoderm being included in the folds. Between the limbs of the folds of the ectoderm are deposited calcareous nodules, similar to, and continuous with, those of the basal plate (see fig. 13). The septa increase in height and thickness as growth proceeds, but always remain covered over by a triple layer of ectoderm, mesogloea, and endoderm, the ectoderm forming the calicoblast layer of the adult polyp. The peripheral extremities of the septa become forked, and, according to von Koch, the forked extremities of adjacent septa unite with one another to form the porous theca.

These statements of von Koch accord very well with certain peculiarities of structure previously observed by him in *Caryophyllia*, *Galaxea lampeyrana*, and *Mussa*, corals belonging to the *Madreporaria aporosa*. He found that in these the theca lies apparently within the body of the polyp, free from the lateral external body wall, and separated from the soft tissues outside by a space which is a part of the coelenteron. The theca is formed by the thickening and fusion of the peripheral ends of the septa and is not a separate structure; where costae are present they are nothing more than continuations of the septa external to the theca. The septa, theca, and costae are everywhere covered by the triple layer of ectoderm (calicoblasts), mesogloea, and endoderm described above. From these relations it will be understood that a portion of the coelenteron lies external to the theca, and this portion may conveniently be described as extrathecal coelenteron. It is divided into chambers by mesenteries corresponding to those which divide the intrathecal coelenteron into radial chambers, the originally continuous mesenteries having been, according to von Koch, cut in two by the fusion of the peripheral ends of the septa, and thus divided into extrathecal and intrathecal portions. The



septa usually project higher into the body cavity than does their product the theca, and the extrathecal mesenteric chambers, (exocœles and entocœles of Fowler) are continuous with the corresponding intrathecal chambers over the lip of the calyx. I have attempted to show these complicated relations in the diagram fig. 14. Fig. 15 exhibits diagrammatically von Koch's view of the formation of the corallum (without epitheca).

It is worthy of remark that, according to von Koch's observations, the basal plate in corals has a different developmental history from the theca, and is morphologically distinct from it. As far as I am aware, no one has yet called attention to this fact. The basal plate, however, is, according to the same author, continuous, if not identical with the structure known as epitheca.

The epitheca is formed in *Astroides* as a secretion of the ectoderm of the body wall at a spot where the lateral walls of the polyp pass into the basal portion; it is connected with the basal plates and form a thin and tolerably smooth lamella investing the lower parts of the polyp (vide fig. 13, *ep.*).

Unfortunately, the further development of the epitheca has not been studied, and we are even deficient of an exact knowledge of its structure in the adult. In his most recent contribution to the subject ('*Morph. Jahrb.*,' xii, 1886, p. 154) von Koch has given a diagram which professes to show clearly all the relations between soft and hard tissues in the adult coral polyp. In it the epitheca is figured as a complete and independent wall of calcareous tissue lying parallel with the theca, and separated from it by a considerable space of extrathecal cœlenteron, this space being bridged over at intervals by the costæ, which in the drawing abut upon and are fused with the epitheca so as to connect it with the remainder of the corallum. Such relations as are shown in this figure occur, as far as I am aware, in no coral either living or extinct; they can only be considered as theoretical, and form a part of the system which von Koch is attempting to construct on the subject of the coral skeleton. I have never seen or heard of a coral in which the soft tissues outside the upper part of the theca are them-



selves invested by a calcareous lamina. In all the forms with a persistent epitheca which I have examined it is invariably in the form of a more or less well-defined layer of calcareous tissue, investing the basal parts of the corallum, and nowhere extending above the level of the soft parts covering the exterior of the latter. Its relations and general appearance suggest its having been formed from the free edge of the soft tissues on the exterior of the corallum, as they retreat farther and farther from the original surface of attachment.

The names exotheca, peritheca, cœnenchyme, epitheca, are all applied to laminar, ring-shaped, or encrusting calcareous investments of the theca, and the distinctions drawn between them are so subtle or so vaguely expressed that I am quite unable to distinguish the difference between them in ordinary cases. In point of fact no essential difference exists. If these structures are deposited by the same parts of the polyp in each case they are morphologically similar to one another; variations of form count for nothing. To determine the mode of formation of corallum, when embryological data are not to hand, a study of the microscopical characters of the corallum by means of sections, and a consideration of the relation of the soft parts to the corallum is necessary. In the first place, it must be kept in mind that throughout the region of the living polyp the corallum is invested by an active secreting layer of calicoblasts. Fowler's figures of *Lophohelia*, and mine of *Mussa*, *Euphyllia*, and *Astræa*, show that there are present in the septa dark lines or centres of calcification marking the central point from which calcification has taken place. In *Mussa* it can be easily seen that concentric layers have been formed around the centre in each septum (fig. 2), and that as two contiguous septa became joined together the area of active secretion was confined to the external or peripheral part of the septum, which therefore increased in length centrifugally. A section taken somewhat lower down than in fig. 2 shows that calcareous tissue is also added over the bridges connecting the septa until they are connected together by a very solid theca. Compare with this section the diagrammatic figure of a coral

(fig. 14) and it will be easily seen that this peripheral thickening of the septa and their fusion to form a theca is due to the activity of the calicoblasts of the inner wall of the extrathecal soft tissues. A reference to Fowler's paper in this number (Pl. I, fig. 5) shows that in *Lophohelia* the sutures become indistinct in the lower sections, owing to the addition of this peripheral ring of calcareous tissue from the inner wall of the "Randplatte," as von Heider calls the extrathecal tissues. The same thing is noticeable, but to a much more marked degree, in *Oculina*, and in it forms the tissue in which the calyces are embedded, i. e. the cœnenchyme. An examination of fig. 6 of this paper shows that in *Euphyllia* (and it is equally true for *Mussa*) that the "Randplatten" of adjacent polyps, where the latter have not separated widely from one another, are continuous, and form a covering for the valley separating the two calices. When in a compound coral all the polyps are thus connected the connection is known as the cœnosarc, and the cœnenchyme is obviously the product of the calicoblasts of the lower layer of the cœnosarc. Fig. 17 is the drawing of a specimen of *Mussa distans* in the Oxford Museum, a species in which the cæspitose type shows a tendency to form a Mæandrine type of colony. Some of the calices are seen to be perfectly separate from one another, and are surrounded by little rings of calcareous matter (*ep.*); whether one calls it peritheca, exotheca, or epitheca does not matter. Where two calices are closely apposed this tissue may be largely developed, and may fill up the valleys completely to the lips of the calices, as in the left-hand corner of the figure (*cœ.*). This is then a cœnenchyme, and a comparison of this figure with fig. 6 must irresistibly lead to the conclusion that the two are formed in one and the same manner. In the one case it is looser and has a more adventitious appearance (*Mussa*), in the other it is more solid and resembles in texture the rest of the corallum (*Caryophyllia oculina*), that is all. The views here expressed accord very well with Professor Martin Duncan's description of epitheca in some serial coralla ('Linn. Soc. Journ.,' xviii, p. 361), and with what is known of its develop-

ment. Beginning at the stage of development drawn in fig. 13 and mentally following the epitheca through its succeeding stages, we see that it is really a basal structure to begin with, and that as growth proceeds it follows the edge of the "Randplatte" as the latter retreats farther and farther from the base. Where a compound colony is formed by lateral budding, and the cœnosarc represents the united "Randplatten" of all the polyps, the epitheca will form a lamellar structure at the bases of the polyps. Where, as in the serial coralla *Porites* and *Leptoria*, the septa of adjacent polyps fuse together, and there is no theca proper separating the interseptal loculi of the two, it can easily be understood how the epithecal nodules described by Professor Duncan would be formed in early stages of growth.

It is obvious from the foregoing that the differences between the tissue which is early laid down to consolidate the theca, and cœnenchyme, and epitheca, depend on quantity and texture, and not on the region of the polyps from which they are formed.

In my description of *Mussa* and *Euphyllia* I have referred to the existence of dissepiments. An examination of figs. 3 and 4 shows that these oblique partitions running across the interseptal loculi are formed from the calicoblasts of what were originally the interseptal parts of the base of the polyp. The soft tissues do not occupy the whole of the cavity of the calyx except in its uppermost part, but slope off to a point below. An examination of fig. 4 shows the relations of these parts to the dissepiments, and fig. 3 shows that the spaces between the dissepiments and the theca are not occupied by any soft tissues whatever. There are probably periods of active coral secretion alternating with periods of reproduction in these polyps. During the latter period the thin dissepiments are formed by the basal tissues, whilst in the former period the septa increase greatly in height, the polyp is, as it were, moved higher up upon its stem, and deserts the old dissepiments upon which it was resting. Then follows a new period of reproduction, during which new dissepiments are

formed. The process is comparable with the formation of tabulæ in the Pocilloporidæ and the growth of Tubipora.

Fowler shows in *Lophohelia*, as I do in *Astræa* (fig. 16), that there are pieces of calcareous tissue intercalated between the peripheral ends of the larger septa, each possessing its own dark centre of calcification. These interstitial pieces, to which Fowler gives the value of true thecal pieces, are clearly formed from the calicoblasts in the angle where the soft tissues dip down between the exsert septa. That this is a region of specially active coral secretion is shown by the large calicoblasts found there by Fowler in *Lophohelia* and myself in *Mussa*. In the highest parts of the calyx, as growth proceeds, these interstitial pieces may develop keels on their inner surfaces which presently project into the calyx as a new cycle of septa (vide fig. 7, *Euphyllia*).

The *Costæ*. — These are clearly shown, from von Koch's account of the development, and from the study of such forms as *Astræa* and *Euphyllia*, to be nothing more than the peripheral ends of the septa projecting beyond the theca. But there are structures called *costæ* in *Madrepora* (Fowler) and *Leptopenus* (Moseley) which do not correspond with the septa, and clearly cannot be continuations of them. Such *costæ* alternate regularly with the septa in *Leptopenus* and in some extinct forms (several species of *Zaphrentis*). In the latter they are said to be epithecal in structure; unfortunately we have no specimens in the Oxford museum which illustrate the point. But, from the figures of *Leptopenus*, I am inclined to think that the so-called *costæ* in this form are epithecal in origin, formed, that is, by the representative of the "Randplatte" in this form (which presumably has the same relations as in *Fungia*). Until we know more about the development of the skeleton in the *Perforata*, it would be rash to dogmatize about the "*costæ*" in *Madrepora*.

I have treated the questions relating to the corallum at length, because every fresh form that is examined convinces me that the expectations formed of founding a new classification of the *Madreporaria* on the anatomy of the polyp are to



meet with disappointment. There is singularly little variation in the forms hitherto examined. Hence I believe that a remodelled classification must depend on a much more intimate study of the structure of the corallum than has hitherto been attempted.

Von Heider ('Zeit. für wiss. Zool.,' xliv, p. 507) recognises this, and attempts to found two new divisions, Euthecalia and Pseudothecalia, on the characters of the corallum.

His Pseudothecalia would include all those forms whose theca is formed by fusion of the peripheral ends of the septa; his Euthecalia all forms in which the theca is a separate and distinct structure (according to him, *Astroides*, and perhaps *Flabellum*). His classification is based upon his account of the structure of *Astroides*, which I cannot accept without further evidence. It stands in direct contradiction to von Koch's account of the development of the same genus. Von Heider states that the corallum is clothed externally by a single layer of ectoderm, mesogloea, and endoderm, the latter layer abutting on the corallum. How then is the corallum external to the polyp, as it undoubtedly is, if von Koch's account of the development be true, and there is no reason to doubt that it is? Thus there is no proper "Randplatte," no extrathecal coelenteron, in *Astroides*, according to von Heider; yet von Koch expressly states that the theca cuts the mesenteries in two, and divides the polyp into an outer moiety and an inner moiety. Finally, in the "Euthecalia" founded on *Astroides*, we learn from development that the theca is formed from the fused ends of the septa; yet, by definition their theca is a distinct structure. Unfortunately the specimens of *Astroides* which I have examined were not well preserved enough to admit of accurate observation. The external surface of all was closely invested by a calcareous sponge, which had in some cases apparently destroyed all traces of polyp external to the corallum. Might not von Heider have been deceived by the existence of a similar sponge on his specimens?

In attempting to collect material for a new classification from the observations already made, we must pay attention



(1) to any marked tendency to departure from a radial symmetry or from the normal Actinian symmetry as shown in the arrangement of the mesenteries; (2) To the presence or absence of a "Randplatte." I am not disposed to attach any importance to exocœlic or entocœlic septa for classificatory purposes, since it appears that in one and the same colony entocœlic septa only, or both exocœlic and entocœlic may be found (*Madrepora*).

With regard to the symmetry. Owing to the presence of "directives," *Actinia* and many *Madreporaria* show a well-marked bilateral symmetry, more marked in the case of many *Madreporaria* by an irregularity in the arrangement of the septa laterally, whereas the regularity is maintained at the ends of the chief axis. But in *Mussa*, *Euphyllia*, and *Lophohelia*, the radial symmetry is perfect; and this is probably a more primitive condition of things. In *Madrepora aspera* there are signs of increased differentiation along the long axis, since there are no filaments on mesenteries 3, 5, 8, 10 (Fowler's numeration), and in *M. Durvillei* there is a strongly marked bilateral symmetry. This symmetry is even more marked in *Seriatopora* and *Pocillopora*, and it can scarcely be doubted that the latter forms are allied to the *Madreporinæ*, although the one family is aporose the other perforate.

Recent researches have made it doubtful whether any sharp distinction can be drawn between the two groups. Von Koch has shown that the septa are formed from the basal ectoderm, and that the theca is formed by fusion of the peripheral ends of the septa in *Astroides*, a perforate *Madreporarian*. A study of the adult anatomy of *Astræa*, *Mussa*, *Lophohelia*, *Euphyllia*, *Fungia*, and others demand a similar explanation. Fowler has shown that a well-developed "Randplatte" with extrathecal mesenteric elements exists in *Rhodopsammia*, a perforate. Where a cœnenchyme with its correlative cœnosarc is present the extrathecal parts of mesenteries are not present. The foregoing part of this discussion has shown that a common cœnosarc is due to nothing more than a persistent connection between the "Randplatten" of adjacent polyps

(vide fig. 6), and that the two structures are homologous. Where a cœnosarc is present it develops a secondary connection with the echinulations of the cœenchyme and is supported on them, the extrathecal part of the mesenteries being at the same time aborted. This is equally the case in the aporose forms *Seriatopora* and *Pocillopora*, and the perforate *Turbinaria* and others. No distinction then can be drawn between aporosa and perforate on account of the presence of a well-developed "Randplatte" containing extrathecal cœlenteron divided up by mesenteries into exocœles and entocœles. The difference between the two groups depends upon the nature of the connection established between the peripheral ends of adjacent septa. It is solid and continuous, an aporose theca is the result; it is loose and trabecular, a perforate theca is formed. The manner in which the mesenteries may be pierced, as it were, by outgrowths from the walls of adjacent septa, is well shown by the formation of synapticula in *Fungia*. In this form processes arise from the walls of the septa which grow towards similar processes from the contiguous septa, and meeting them fuse with them to form synapticula. This may easily be understood by a study of a carefully macerated corallum. I have shown that the mesenteries are actually perforated by these synapticula, and that a simple canal system exists connecting the extrathecal with the intrathecal cœlenteron. This process is carried out further and in a more complicated manner in the perforate. My researches on *Fungia* have shown that the elevation of the *Fungidæ* into a group *Fungida* is altogether groundless. Their anatomy does not differ from that of other *Madreporaria* either in the arrangement of tentacles, as Dana erroneously described, or in the internal structure as Professor Duncan inferred from Professor Moseley's perfectly correct description of the soft parts of a *Bathyaectis* after decalcification. I have not yet had the opportunity of investigating *Bathyaectis*, but Professor Moseley's description of the appearance of its soft parts after decalcification exactly tallies with the appearance of *Fungia* under the same circumstances.

The one form which must be placed in a separate group is Flabellum. It possesses no "Randplatte," its calyx therefore cannot grow peripherally, and in section it presents an entirely different appearance to any other coral. Fowler gives accurate drawings of sections of Flabellum in his latest paper ("Anatomy of the Madreporaria," iii), and it is not worth while to reproduce them. His explanation, however, is not quite adequate to explain the phenomena. If we assume that Flabellum develops on the type of Astroides—and from the anatomy of the adult we have no right to assume that it develops otherwise, it is impossible to see how the theca could have been formed by fusion of the peripheral ends of the septa, and yet no soft parts left external to the theca. To understand this the reader must mentally follow the processes of growth with the aid of figs. 13, 14, and 15, up to the adult condition. My view of the so-called theca of Flabellum is that it is really a basal structure which has grown upwards to form a calyx, in a manner analogous to the opposite process by which the theca of *Fungia* has flattened out to form an apparent basal structure. The base would always lie actually, as well as apparently, external to the polyp, and would entirely enclose it. It could only be added to on its inner side, and thus Fowler's interpretation of the appearance of the centres of calcification would continue to hold good. Moreover, the peculiar appearance of infolding towards the centres of the septa, figured but not discussed by him, would receive a sufficient explanation when we consider that the septa are formed continuously with the basal plate, and within folds of the three layers, each of which necessarily includes two layers of calicoblasts. The form of the corallum exhibits in fact the relation of the primary folds of tissue within which the septa are developed. The sutures—which, it must be observed, do not reach to the exterior of the "theca"—would necessarily result from the further growth of the septa. If I am right in considering epitheca to be continuous with and indistinguishable from the basal plate, my views on Flabellum coincide curiously with those of von Koch, who regards the apparent

theca of Flabellum as epitheca, much as I disagree with many of his expressed views on epithelial structures.

The only arrangement, then, which our present knowledge of the Madreporaria permits us to make, is as follows:

1. Madreporaria with no directive mesenteries and a perfectly radial symmetry, Lophohelia, Mussa, Euphyllia.

2. Madreporaria with directive mesenteries and a combined radial and bilateral symmetry, Turbinaria, Rhodopsammia, Fungia, and many others.

3. Madreporaria with reduced radial symmetry and marked bilateral arrangement of parts, Madrepora, Pocillopora, Seriatopora.

4. Madreporaria with a basal pseudotheca and no "Randplatte," Flabellum.

I do not pretend that this arrangement has the value of even an incomplete natural classification, but it is the best arrangement that the facts warrant us in making. Finally, it must be observed that the skeleton of the Madreporaria differs widely from that of Alcyonaria. In the former the calcareous tissue is nearly certainly elaborated and secreted by the ectodermic cells; it is always external to the polyp. In the latter, ectodermic cells early separate from their primitive position, become embedded in the mesogloea, and develop spicules within their substance. The skeleton then is within the polyp. In some cases skeletal structures may in the latter group be developed within endoderm cells (E. B. Wilson, "The development of Renilla," "Phil. Trans.," clxxiv, p. 723).

Unsatisfactory as the conclusions as to classification given above may be, I hope that I have succeeded in presenting the facts known about the morphology of the Madreporaria in a manner comprehensive enough to be of use to future investigators in a difficult field.



## EXPLANATION OF PLATES III &amp; IV.

Illustrating Mr. G. C. Bourne's paper "On the Anatomy of Mussa and Euphyllia, and the Morphology of the Madreporarian Skeleton."

FIG. 1.—Portion of a colony of *Mussa corymbosa*, of which the polyps are retracted and shrunk by the action of alcohol. Half natural size. *r.* Limit of soft tissues external to the corallum. (Randplatte of von Heider.)

FIG. 2.—Transverse section of the calyx of *Mussa corymbosa*, showing two principal and one secondary septum. The dark lines or areas are centres of calcification, and around them are concentric lines of growth. *s. s.* Sutures. *d.* Dissepiments.

FIG. 3.—Transverse section across a single polyp of *Mussa corymbosa*, to show the arrangement of the septa and dissepiments. The corallum is represented in white and the soft tissues in black. The spaces between the dissepiments and the theca not occupied by any soft tissues are shaded. *th.* Theca. *sp*<sup>1</sup>. Principal septa. *sp*<sup>2</sup>. Secondary septa. *d.* Dissepiments. *r.* Randplatte.

FIG. 4.—Diagram of a longitudinal section through *Mussa corymbosa*. On the right side the section passes close to one of the principal septa. On the left side a mesentery is exposed. The mesogloea is represented in black, the ectoderm shaded with vertical lines. *st.* Stomodæum. *ec.* Ectoderm. *mg.* Mesogloea. *en.* Endoderm. *cy.* Calicoblast layer. *mf.* Mesenterial filaments. *m.* Mesentery, with longitudinal muscles. *r.* Randplatte. *d.* Dissepiments.

FIG. 5.—Part of a transverse section through the hard and soft parts of *Mussa corymbosa*, just below the level of the stomodæum. The section comprises one of the ends of the long axis of the polyp. Mesogloea, ectoderm, and endoderm shaded as in Fig. 4. *m'*. Extrathecal portions of the mesenteries. *mc.* Pleats of mesogloea, to which the mesenterial muscles are attached. Remainder of the lettering as in Fig. 4.

FIG. 6.—*Euphyllia glabrescens*, natural size, showing the expanded polyp and the extension of the Randplatte over the lip of the calyx. At *x* the Randplatten of adjacent polyps are seen to be continuous, forming a cœnosarc. *r.* Limit of the Randplatte.

FIG. 7.—Transverse section through the calyx of *Euphyllia glabrescens*, showing primary (*sp*<sup>1</sup>), secondary (*sp*<sup>2</sup>), and tertiary (*sp*<sup>3</sup>) septa. The centres of calcification are shown by dark lines. *s. s.* Sutures. *d.* Dissepiments.



FIG. 8.—Part of a transverse section through a decalcified polyp of *Euphyllia glabrescens*. This section shows the Randplatte *r*, including the extrathecal cœlenteron and the extrathecal portions of the mesenteries, *m'*. The endoderm, *en'*, of the intrathecal part of the polyp is greatly vacuolated, forming a reticular tissue, which fills up the whole of the cœlenteron and contains in its meshes zooxanthellæ and nematocysts. The stomodæal canals, *st. c.*, occupy the axial part of the polyp, and serve as the digestive cavity. *ov.* Ova. *n. c.* Nutritive cells.

FIG. 9.—Developing nematocyst from the stomodæum of *Euphyllia glabrescens*. Magnified 750.

FIG. 10.—Ripe nematocyst from the stomodæum of *Euphyllia glabrescens*, with the axis tube everted, but the thread not ejected. Magnified 750.

FIG. 11.—A nematocyst similar to that in Fig. 10, but with the thread only ejected, showing the armature at the tip of the latter.

FIG. 12.—A nematocyst from the endoderm of *Euphyllia glabrescens*.

FIG. 13.—Longitudinal section through an *Astroides* embryo, copied from von Koch, showing the basal plate, *bp.*, being formed from the ectoderm (calicoblast layer) of the base of the polyp, and a septum, *sp.*, in the process of formation. The epitheca, *ep.*, is seen at the base of the polyp. *z.* The piece of cork on which the embryo rests.

FIG. 14.—Diagram to exhibit the relations of the polyp to the corallum. *T. T.* Tentacles. *ec.* Ectoderm. *mg.* Mesogloea. *en.* Endoderm. *st.* Stomodæum. *mf.* Mesenterial filaments. *r.* Randplatte. *m.* Mesentery. *m'*. Extrathecal portion of mesentery. *th.* Theca. *Bp.* Basal plate. *ep.* Epitheca.

FIG. 15.—Diagram to exhibit the formation of the theca from the fused peripheral ends of the septa. *cm.* Columella. Remainder of the lettering as in Fig. 14.

FIG. 16.—Section across the calyx of *Astrea cavernosa*, showing alternately larger (*sp*<sup>1</sup>.) and smaller (*sp*<sup>2</sup>.) septa. In each septum can be seen the dark centres of growth and the sutures, *s.*, marking off contiguous septa from one another. *t. th.* Intercalated pieces lying between the ends of the septa (true thecal pieces?).

FIG. 17.—*Mussa distans*. In this specimen the corallites may in some instances be seen standing apart, in which case their lower portions are covered by a loose epitheca, *ep.* In other places the corallites are set closer together, and the valleys between them are partially filled up by a loose epitheca. In, yet other places the calices are completely soldered together by epitheca, *cæ.* which fills up the valleys to the lips of the calices, and has the same functions and relations as coenenchyme.



## On the Intra-Ovarian Egg of Some Osseous Fishes.

By  
**Robert Scharff, Ph.D., B.Sc.**

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With Plate V.

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THE following researches were carried out during the past summer while acting as assistant to Professor McIntosh, at the St. Andrew's Marine Laboratory. The fresh material for the investigations was taken from St. Andrew's Bay, which is extremely rich in all kinds of animal life. Professor McIntosh kindly placed at my disposal many preserved ovaries and ova from his large collection, which served me for sections. But my contributions to the history of development leave a good many gaps to be filled up by future observers, as I was not able to obtain a consecutive series of the ovaries of any species. If an ovary be opened it is generally found to contain eggs of a certain size only, and in order to get an entire succession of the various stages, ovaries of the same species should be procured at different seasons of the year. It is not possible to see all the phases of development in one and the same ovary. There is one form, however, which abounds near St. Andrews, and which, due to its spawning period being spread over several months, contains ova of almost all sizes. This is the gurnard (*Trigla gurnardus*). It is in many other points a very suitable object for investigation.

The following is a list of the species of fishes whose ova or ovaries I examined:—*Trigla gurnardus*, *Gadus virens*, *G. æglefinus*, *G. luscus*, *G. merlangus*, *Lophius*

piscatorius, *Salmo salar*, *Anarrhichas lupus*, *Conger vulgaris*, *Blennius pholis*, *Hippoglossoides limandoides*.

In several cases the investigation was carried out on fresh ovaries; others were only inspected in a preserved condition. I cut sections of all of them. They were hardened in weak chromic or in picrosulphuric acid.

With regard to the result of my researches, I may mention that there were two features which seemed to me of special interest. Firstly, the development of the yolk, and secondly, the origin of the egg-membranes and the follicle. I think I have been successful in tracing the first, and also answered part of the latter question. But the smallness of the objects presents great difficulties, and the ova, after they pass a certain size, become so opaque that their structure has to be studied entirely from sections of hardened specimens. I propose to divide this paper into five chapters, beginning with the nucleus and its changes, and finishing up with a general account of the development of the intra-ovarian egg. An abstract of this paper was read before the Royal Society at their meeting in the beginning of December last. It will be found in this year's Proceedings of the Society.

The various stages of the growing ovum have all, or nearly all, been seen in the gurnard's egg; but, in order to show that they also occur in the other forms, where it was possible, illustrations have been copied from sections of the different species examined.

## I. THE NUCLEUS AND ITS CHANGES IN THE SMALLER OVA.

I found the smallest ova, measuring 0.011 mm. in diameter, in the ovary of the Haddock. In these eggs the nucleus occupies almost the whole of the interior (fig. 1). A very narrow zone of protoplasm, which, as far as I could ascertain, was not bounded by a membrane, surrounded the nucleus. The wall-less ovum lies in the endothelial or connective tissue

stroma of the ovary. The nucleoli (fig. 1, *n'*)—there are a great number of them—rest as a rule on the inner surface of the nuclear wall, barring a few, which take up a central position. With an ordinary high power (Zeiss F<sup>4</sup>) nothing more of an internal structure can be detected.

The next size (fig. 2) shows a division of the protoplasm into two distinct layers or zones, an outer lighter and an inner darker or more denser one. The egg in this stage is still tolerably transparent. Fig. 2 represents a small gurnard's egg (*Trigla gurnardus*) 0.030 mm. in diameter. The nucleoli show an inclination to gather still more towards the periphery of the nucleus, and the central portion rarely reveals a germinal spot, while there appears instead an intra-nuclear network which will be more minutely described in larger eggs. In ova of this bulk, and also in somewhat larger ones, one or more of the nucleoli become larger than the others, and in their interior highly refractive specks are visible which have sometimes been described as endonucleoli. Another peculiarity about the large germinal spots is that they are always surrounded by a light portion which does not stain with carmine.

In somewhat larger ova, of a diameter of 0.080 mm. (fig. 3), the dark zone round the nucleus is seen to have increased considerably while the light one remained stationary. The large nucleus which is represented in fig. 4 shows that in some cases the big nucleoli disappear almost completely, leaving an unstained part around them. Frequently one spot was seen in the centre of the nucleus among what is generally known as the "chromatic" substance. This consists of very minute granules distinguished from the rest of the nuclear substance by its greater consistence, a higher refractive power, as well as by its capability of assuming a strong tint in certain solutions of colouring matter which are used among microscopists for staining nuclei. The small granules are suspended in a network of threads, which has so often been described in both animal and vegetable cells, and which plays a conspicuous part in the karyokinetic figures of the dividing nucleus. It is



specially well seen in fig. 9, *n. f.*, representing a nucleus and its surrounding protoplasm of a middle-sized gurnard's egg.

I agree with my friend Dr. Will in not attaching any morphological significance to the nucleoli. They must be regarded as large masses of chromatic substance. In some instances they are entirely absent; in others one or more may be present.

To return to the large nucleoli which, as has been mentioned, are occasionally present in the ova of the gurnard, they are never wanting in the eggs of the conger eel (*Conger vulgaris*). They stain slightly darker than the small ones. In several cases (fig. 5, *n'*) I noticed a small nucleolus being constricted off from a large one. In an egg of *Gadus virens* (fig. 6), measuring 0.105 mm. in diameter, the dark protoplasm (*pr.*<sup>1</sup>) surrounding the nucleus in smaller ova had been separated in form of a ring, and internally to it another narrower ring (*pr.*<sup>2</sup>) of protoplasm was frequently present. The zone of light protoplasm externally had increased considerably meanwhile. In some instances, however, the dark zone had invested the whole of the ovum, and the light portion had entirely disappeared. Another feature which came under my notice now was that the dark zone contained the faint outlines of spots corresponding in size to nucleoli (fig. 7, *sp.*), none of which, however, were seen outside in the light protoplasm. Only in *Hippoglossoides* did I occasionally observe similar spots close to the surface of the egg.

There can be little doubt that these spots are nucleoli which have travelled through the nuclear membrane into the surrounding protoplasm, and are gradually dissolved there. I notice here incidentally that possibly some find their way to the surface of the egg to form the nuclei of the follicular epithelium. This is only a supposition; but it will be referred to again more fully in a subsequent chapter.

In a larger egg of *Gadus virens*, 0.132 mm. in diameter (fig. 7), we still find a granular protoplasmic ring round the nucleus; however, a great change has come over the nucleoli, which are now no more closely attached to the nuclear wall. They seem to have become broken up or dissolved in some

way, assuming all sorts of shapes. Some are crescent-shaped, some are like rods, and others again are reduced to small specks or angular fragments. Now what is the significance of all this?

To commence with the relation of the dark protoplasm towards the light one, I may previously state that this division of the contents of the ovum has been seen by several authors not only in fishes and amphibians, but also in invertebrate forms. Bambeke<sup>1</sup> observed a division of the protoplasm into two zones in the young ova of *Leuciscus rutilus*, *Hippocampus antiquorum*, and *Lota vulgaris*. Eimer<sup>2</sup> believes in the identity of His' "Rindenschicht" with His' "Zonoid layer;" his figures, however, show clearly that in young ova, at any rate, it corresponds to the light protoplasm which I described, in distinction to the more granular part internally to it. The fact that the yolk is divided into zones has also been observed in *Sepia* by Lankester.<sup>3</sup> Finally, my friend Dr. Will<sup>4</sup> has noticed the same phenomenon in *Orthoptera*. No doubt the formation of protoplasmic rings round the nucleus of the growing egg has been seen in a still greater number of animal groups than I have just enumerated.

I think there can be little hesitation in regarding the dark central protoplasm as owing its origin to the nucleus, although there appear to be cases, such as recorded by Lankester,<sup>3</sup> in which the protoplasm is nourished entirely from without.

But a difficulty presents itself here. Has the dark part originated by a simple transformation of the light portion, or has another substance been added to the protoplasm from the nucleus causing this change? The latter seems the most probable of the two cases. This view is considerably strength-

<sup>1</sup> Bambeke, "Recherches sur l'embryologie des poissons osseux," 'Mém. cour. Acad. Belg.,' vol. xi, 1875.

<sup>2</sup> Eimer, "Untersuchungen über d. Ei d. Reptilien und Fische," 'Archiv f. mikr. Anat.,' vol. viii, 1872.

<sup>3</sup> Lankester, E. Ray, "Contributions to the Developmental History of the Mollusca," 'Philosophical Transactions,' 1875.

<sup>4</sup> Will, "Bildungsgeschichte und morphologischer Werth. d. Eies von *Nepa* und *Notonecta*," 'Zeitschrift f. wiss. Zool.,' vol. xli, 1885.

ened by an observation which was published by Ransom<sup>1</sup> in 1867, in the 'Philosophical Transactions.' He says: "The action of the water is not the same on the free uninjured germinal vesicle in young ova as it is on those still within the egg. I found that the results were in a great measure due to the influence exerted by the constituents of the yolk, which were carried into the vesicle by osmose. When the ovum was acted upon by water, the germinal spots were gradually seen to become pale, and finally disappear. These facts strongly suggest the notion that the germinal spots are soluble in some of the constituents of the yolk, and we may thus explain their disappearance in ripe ova.

Ransom likewise observed that in the earlier ovum of *Gasterosteus leiverus* and *pungitis*—the two species which he examined—the germinal spots, which were embedded in the colloid matrix of the vesicle, were to be seen at the periphery of the vesicle only, so as to be in contact with the inner surface of the nuclear wall. The germinal spots were often "tailed and vacuolate."

In an older stage, such as that represented by fig. 8, the dark ring encompassing the nucleus has evidently been absorbed, and the latter has diminished in size while the egg itself has continued to grow larger. Indications of the boundary of the old germinal vesicle are still seen (fig. 9, *n'*.), and the space between it and the reduced one is filled with dark granular protoplasm, which seems still to be produced by the action of the nucleus. A new process, however, begins at this stage, namely, the formation of the yolk spherules, which will be described in the next paragraph.

## II. THE LARGER OVA AND THE FORMATION OF THE YOLK SPHERULES.

If we look at figure 9, which represents the nucleus of a large egg surrounded by a zone of protoplasm indicating the

<sup>1</sup> Ransom, "Observations on the Ovum of Osseous Fishes," 'Phil. Transactions,' vol. clvii, 1867.

outlines of its predecessor, we are at once struck by the peculiar protuberances which make their appearance all over its outer surface. They were best seen in sections through the hardened ova of the gurnard. These measured somewhere about 0.130 mm. in diameter. These diverticula, buds or "stolons," as they have been called by Balbiani, are pushed out by the nucleus. Part of the nucleoli resting upon the diverticula is drawn into them and carried away towards the exterior of the egg. They have the appearance now of minute vesicles or cells containing a nucleus. For such, indeed, they have been mistaken even by the most recent writer on the subject, Ovsiannikov. The vesicle is either a portion of the nuclear wall which has become constricted off, or it may be a later formation. Sometimes the vesicles thus formed do not contain any nucleolar matter and remain unaffected by staining reagents. Like the others they travel towards, but they do not quite reach the surface of the egg, leaving a cortical layer of protoplasm which is the "Rindenschicht" of His. The vesicles with their nucleolar contents are the yolk-spherules. The solid mass in their interior soon breaks up into fine granules, and it is in this condition that the yolk-spherules are found in the largest intra-ovarian eggs. The granules, however, are at first of a dark colour, which they only lose on the ovum becoming ripe. In the mature egg the yolk is perfectly transparent.

The nuclear network which has been mentioned above is specially well seen at this stage (Fig. 9, *n.f.*). The threads connecting the minute granules in the interior of the nucleus seem to be made up of fine dots rather than solid fibres.

The vesicles with clear contents might possibly be what is known as "oil globules," on the significance of which my friend Mr. Prince<sup>1</sup> has recently published an interesting paper. Their oily contents would thus originate from the clear nuclear substance. I merely throw this out as a suggestion, but if it should ultimately be proved correct, it would form another addition to these most interesting and instructive phenomena which the

<sup>1</sup> Prince, Ed. E., "On the Presence of Oleaginous Spheres in the Yolk of Teleostean Ova," 'Ann. Nat. Hist.,' 1886.



ovum of osseous fishes is undergoing during its growth. In the ripe gurnard's egg a large oil-globule is to be found at the periphery of the yoke, and similar ones occur in many other marine Teleosteans. The largest yoke spherules in the gurnard (fig. 10) have a diameter of 0.015 mm. In the frog-fish (*Lophius piscatorius*), however, their size varies from 0.018 up to 0.090 mm. (fig. 11). The contents in the latter case consist, besides the small granules, of peculiar crescent-shaped bodies and vacuoles. In many of them dark crystalline bodies were seen enclosed in a vesicle. Ovsiannikov<sup>1</sup> likewise makes mention of crystals and peculiar oval bodies as occurring in the yolk spherules of *Osmerus eperlanus*.

With regard to the process of budding from the nucleus which I just described as leading to the origin of the yolk-spherules, similar changes of the nucleus have been noticed by various observers; but only Will<sup>2</sup> derives the yolk-spherules from these buds. He investigated the intra-ovarian egg of *Amphibia*. No other writer seems to have seen anything corresponding to this process in Vertebrates. Roule,<sup>3</sup> Fol,<sup>4</sup> and Balbiani<sup>5</sup> also describe the formation of diverticula from the surface of the nucleus. The first two studied the ova of *Ascidians*, the latter those of *Myriapods*. However, the ultimate fate of these diverticula containing nucleolar portions is to become cells of the follicular epithelium, which in Teleostean ova has been formed before those changes began. That the yolk-spherules originate within the egg has been rigorously maintained by some of the greatest authorities, such as Balfour and Gegenbaur, but neither of the two mentions the budding

<sup>1</sup> Ovsiannikov, "Studien über d. Ei hauptsächlich d. Knochenfische," 'Mém. Acad. Imp. St. Petersb.,' vol. xxxiii, 1886.

<sup>2</sup> Will, "Ueber d. Entstehung d. Dotters und d. Epithelzellen bei Amphibien und Insekten," 'Zoologischer Anzeiger,' 1884.

<sup>3</sup> Roule, "La structure de l'ovaire et la formation des œufs chez les Phalusiadées," 'Comptes Rendus,' 1883.

<sup>4</sup> Fol, "Sur l'origine des cellules du follicule chez les Ascidiens," 'Comptes Rendus,' 1883.

<sup>5</sup> Balbiani, "Sur l'origine des cellules du follicule chez les Géophiles," 'Zoologischer Anzeiger,' 1883.

process of the nucleus. Balfour<sup>1</sup> writes on this subject: "Yolk-spherules arise as extremely minute, highly-refracting particles in a stratum of protoplasm some little way below the surface, and are always most numerous at the pole opposite the germinal vesicle." "It deserves to be specially noted that when the yolk-spherules are first formed, the peripheral layer of the ovum is entirely free from them." "Two points about the spherules appear clearly to point to their being developed in the protoplasm of the ovum, and not in the follicular epithelium. 1. That they do not make their appearance in the superficial stratum of the ovum. 2. That no yolk-spherules are present in the cells of the follicular epithelium, in which they could not fail to be detected." Balfour's opinion is that Gegenbaur's<sup>2</sup> account of the formation of the yolk-spherules in birds is probably correct. "Protoplasmic molecules," says Gegenbaur, grow into larger granules. These become larger again, and are transformed into vesicles, which increase continuously in volume. New solid products now take their origin in the interior, and dissolve into fine granules." "The yolk-spherules originate in the interior of the egg, and not from the follicular epithelium." These observations, which were made in birds', agree with those in reptiles' eggs.

On the other hand, yolk-spherules appear also sometimes to be formed from without. At any rate,<sup>3</sup> Beddard regards it as highly probable. His view, which was deduced from the study of the ovarian ovum of *Lepidosiren* (*Protopterus*), is supported, among other facts, by their being no external membrane in this stage. The follicle lies immediately on the yolk, and masses of migrating cells were seen in course of being budded off from it.

To return to the nucleus again; it rapidly degenerates as

<sup>1</sup> Balfour, F., "Structure and Development of the Vertebrate Ovum," 'Quart. Journ. Micr. Sci.,' vol. xviii, 1878.

<sup>2</sup> Gegenbaur, "Ueber d. Bau und d. Entwicklung d. Wirbelthier Eier mit partieller Dottertheilung," 'Müller's Archiv,' 1861.

<sup>3</sup> Beddard, F., "Observations on the Ovarian Ovum of *Lepidosiren*," 'Proceedings of the Zoolog. Soc.,' 1886.

the egg grows older. Whether the variously shaped particles of the remaining nucleoli, which we have seen in figure 7, subsequently congregate in the centre, in order to become round again, I have not been able to observe. Such a transformation, however, according to Iwakawa,<sup>1</sup> seems to obtain in the young ova of Triton. At any rate the nucleus becomes smaller and smaller, to the benefit of the yolk. In an almost ripe ovum very little of it is left (fig. 12). It then lies eccentrically, and consists of clear contents, with the exception of a few round nucleoli. More of the latter are seen just outside the nucleus in the surrounding yolk. Large vacuoles (*va.*) have also made their appearance in the immediate neighbourhood of the nucleus, but their presence may be due to the fixing reagent. It is important to note that no trace of a membrane can be made out at this stage of the germinal vesicle.

The gradual decomposition of the nucleus in the growing egg has been seen by many authors, and we have descriptions not only from vertebrate, but also from invertebrate ova. Thus Hertwig,<sup>2</sup> in his researches on the formation of the egg in *Toxopneustes lividus*, says, "When the ovum becomes ripe, the nucleus undergoes regressive metamorphosis, and is driven by means of protoplasmic contractions to the surface of the yolk. Its membrane dissolves, and its contents break up and are reabsorbed by the yolk. The nucleolus, however, seems to remain unchanged, and appears to travel into the yolk mass, becoming the permanent nucleus of the ripe ovum."

With regard to the question as to the presence or absence of a membrane in the nucleus, I could see a double contour distinctly in the section represented by figure 7. I believe it is now generally recognised that the nucleus is surrounded by a membrane, and most of the references I can find support this fact. Thus Hertwig, in the paper quoted above, speaks of the

<sup>1</sup> Iwakawa, "The Genesis of the Egg in Triton," 'Quart. Journ. Micr. Sc.,' vol. xxii, 1882.

<sup>2</sup> Hertwig, "Bildung d. thierischen Eies," 'Morphol. Jahrbuch,' vol. i, 1875.

nuclear membrane as being of a distinct double contour and well defined from the surrounding part, as well as from the contents of the nucleus. I could cite many other authorities, but it would lead me too far.

### III. THE EGG-MEMBRANES.

At the recent meeting of the British Association at Birmingham, I submitted a paper on the egg-membranes of osseous fishes. I pointed out that, in a section of the gurnard's egg, I had seen a thin membrane internally to the egg capsule or "zona radiata," and that it had been already noticed by Ransom and other observers.

I think the egg-membranes constitute that part of the Teleostean ovum on which most has been written. I shall attempt to throw some light on the discrepancies which we find among zoologists in regard to these membranes. All zoologists agree as to the existence of one more or less thick layer, which most of them believe to be pierced by minute pores. Now I find that this layer has no less than seven different names, as will be seen by the subjoined list :

1. *Zona radiata*.—Balfour, Beneden, Brock, McIntosh, Orsiannikov, Reichert, Solger.
2. *Vitell. membr.*—Aubert, Beddard (?), Cunningham, Haeckel, Kölliker, Waldeyer.
3. *Egg-capsule*.—His, Müller, Prince.
4. *Yolk-sac*.—Ransom.
5. *Zona pellucida*.—Eimer.
6. *Chorion*.—Leuckart, Rathke.
7. *Egg-shell*.—Oellacher, Vogt.

Leaving out the follicular layer, or "granulosa" as it has been called especially by continental investigators, we have besides the above-mentioned membrane, descriptions of one or two or even three others. As I am here only dealing with the intra-ovarian egg of a few marine forms, some of which were not even ripe enough to possess egg-membranes, my observations will necessarily be somewhat incomplete in this respect. I will commence with a description of the "zona radiata,"



following Balfour and others in adopting this name for the principal membrane. As it is probably in all cases pierced by radiating pores, the term "zona radiata" indicates its most prominent morphological character. The name "vitelline membrane" is misleading, additional membranes having been described, some of which no doubt owe their origin also to the vitellus. I believe one of the principal causes of the very great divergence of opinion as to the number of membranes, is that in some cases only intra-ovarian and in others ripe ova have been examined. Balfour<sup>1</sup> has shown in his careful researches on the intra-ovarian egg of Elasmobranchs, that in many cases an absorption of part or the whole of the membranes takes place. The disappearance of the "zonoid layer" in the ripe ovum of the gurnard, shows that such an absorption may also occur in Teleosteans. The ova of Lepidosiren, described by Beddard,<sup>2</sup> afford another example of an imbibition of the membrane taking place. I may mention here incidentally that I am inclined to look upon his zona radiata as the above-mentioned zonoid layer.

In *Trigla gurnardus* the zona radiata in section does not show a distinct striation, but in the fresh egg it is well visible. Its thickness (figs. 8, 13, 14, 15, *z.*) averages about 0.008 mm. It is often granular and stains darkly as a rule in carmine and hæmatoxylin. Internally to it is a much broader layer (figs. 8, 13, 14, 30), which in section appears to be the inner portion of the zona, the stripes being apparently continued through both. The width of the latter is about 0.025 mm. Both layers are striped, i. e. provided with minute radial pores. I was inclined at first to consider these two layers as belonging to one membrane, namely, the "zona radiata."

However, its semi-fluid condition distinguishes it from the much firmer and elastic zona radiata. Hitherto it has always been looked upon as the outer portion of the yolk, and has been described by Gegenbaur in the ova of birds, reptiles, and Elasmobranchs as the "helle Randschicht," and by His as the

<sup>1</sup> Balfour, loc. cit.

<sup>2</sup> Beddard, loc. cit.

“zonoid layer.” It stains only slightly, and I have found it as a rule devoid of granules or vesicles. In the ripe ova this zonoid layer disappears entirely. I cannot agree with His, according to whom it is replaced by the egg-capsule or zona, as the latter is always formed before the zonoid layer.

Brock<sup>1</sup> thinks that this thick layer is a peculiarity, probably in some relation to the nourishment and growth of the egg.

According to Kupffer,<sup>2</sup> the membrane surrounding the yolk in the herring's egg consists of two layers, viz. an inner finely striated and an outer one into which the striæ are not continued. The striæ, he says, might be radial pores, however, he must point out that, as the pores are not found in the external layer, they certainly do not open exteriorly. Eimer<sup>3</sup> first noticed the stripes in the zonoid layer, which he believes are due to processes from the follicle. He saw the stripes in *Alburnus lucidus*, *Salmo fario*, and *Perca fluviatilis*, but they only occupied the outer half and are not so delicate as those in the zona. That this layer belongs to the yolk, he says, is seen by the fact that in separating it follows always the latter. My own observations are in direct opposition to this last statement. Eimer also speaks of a membrane externally to the zona. He believes that it originates from the follicular layer and therefore might be looked upon as a chorion.

The same author regards the radial striation in the zona radiata as being due to little rods between which are found pores. He likewise examined the ovum of Reptiles, in which he noticed besides the zona and the external “chorion,” an internal membrane, of which I shall have to speak presently.

Kölliker<sup>4</sup> says “there is in all fishes' eggs an outer, more resistant, thinner layer externally to the zona which may even preserve the striation in some cases.

<sup>1</sup> Brock, “Beiträge z. Anatomie und Histologie d. Geschlechtsorgane d. Knochenfische,” ‘Morphol. Jahrbuch,’ vol. iv, 1878.

<sup>2</sup> Kupffer, ‘Die Entwicklung d. Herings im Ei,’ Berlin, 1878.

<sup>3</sup> Eimer, “Untersuchungen über d. Ei d. Reptilien und Fische,” ‘Archiv f. Mikr. Anatomie,’ vol. viii, 1872.

<sup>4</sup> Kölliker, “Untersuchungen z. vergleichenden Gewebelehre (also on Ovum),” ‘Verhandl. d. Phys. Medic. Gesellschaft,’ Würzburg,’ vol. viii, 1858.

Leuckart<sup>1</sup> makes mention of an outer membrane-like boundary of the zona, through which canals are continued, and Aubert<sup>2</sup> as well as Remak<sup>3</sup> speak to the same effect.

A few other observers such as His, Lereboullet,<sup>4</sup> Solger,<sup>5</sup> and Ransom,<sup>6</sup> do not make any reference to a layer externally to the zona, but admitting at the same time the porous structure of the latter; while Haeckel,<sup>7</sup> speaks of a structureless vitelline membrane only, having delicate dark spots. Ovsiannikov<sup>8</sup> again, the most recent writer on the ova of osseous fishes, mentions three layers as occurring in *Perca fluviatilis*. Prolongations from the follicular cells into the canals of the zona were seen distinctly. No doubt they serve for nourishing the egg. There is a distinct zona radiata externa in *Osmerus eperlanus*, while in *Gasterosteus* there is only one layer.

Lindgren,<sup>9</sup> who has recently examined the structure of the mammalian ovum, found that the zona pellucida, which corresponds to our zona radiata, is pretty often completely homogeneous in ripe eggs. He believes that this is due to different physiological conditions of the egg. Author used the highest powers available.

Johann Müller<sup>10</sup> was to my knowledge the first to identify

<sup>1</sup> Leuckart, "Ueber die Mikropyle bei Insekteneiern (also Fishes)," 'Müller's Archiv,' 1855.

<sup>2</sup> Aubert, "Beiträge z. Entwicklungsgeschichte d. Fische," 'Zeitsch. f. wiss Zool.,' vol. v, 1854.

<sup>3</sup> Remak, "Ueber Eihüllen und Spermatozoen," 'Müller's Archiv,' 1855.

<sup>4</sup> Lereboullet, "Résumé d'un travail d'embryologie comparée sur le dével. du brochet, &c.," 'Ann. Sci. Nat.,' vol. i, 4th ser., 1854.

<sup>5</sup> Solger, "Dottertropfen in d. intracapsulären Flüssigkeit v. Fischeiern," 'Arch. f. Mikr. Anat.,' vol. xxvi.

<sup>6</sup> Ransom, loc. cit.

<sup>7</sup> Haeckel, "Ueber d. Eier d. Scomberesoces," 'Müller's Archiv,' 1855.

<sup>8</sup> Ovsiannikov, loc. cit.

<sup>9</sup> Lindgren, "Ueber d. Vorhandensein v. wirklichen Porenkanälchen in d. Zona pellucida v. Säugethieren," 'Arch. f. Anat. und Phys. Anat. Abth.,' 1877.

<sup>10</sup> Müller, "Ueber Zahlreiche Porenkanäle in d. Ei-Kapsel d. Fische," 'Müller's Archiv,' 1854.

the punctures on the surface of the zona radiata with pores piercing it. Since then, although we occasionally find statements to the contrary, the great bulk of zoologists maintain that pores exist in all cases. May not the fact that some of the recent observers have not noticed them be due to the peculiar physiological condition of the egg which Lindgren referred to? Careful investigation of a large number of both intra- and extra-ovarian ova of marine fishes would no doubt help to clear up the matter.

In the zona radiata of the ripe egg of *Gadus morrhua* (spirit preparations) no trace of a striation could be made out with a magnifying power of about 800 diam. Cunningham,<sup>1</sup> however, has seen the stripes in ova of the same species which were prepared with Perenyi's fluid, and I firmly believe they exist in all cases. As the same observer has recently pointed out, the pores may occasionally (*Myxine glutinosa*) be branched.

To return to His' zonoid layer, I stated my reasons for considering it as one of the egg-membranes, although all previous observers looked upon it merely as the modified external part of the yolk.

The ova of *Blennius pholis* have one layer only. The zonoid layer is always absent.

In speaking of the zonoid layer, His<sup>2</sup> says "It is probable that it belongs to the zona radiata, but the detailed history of both formations has still to be done."

A question which has occupied the attention of many modern observers on this subject is whether the pores of the zona radiata receive processes from the surrounding follicular cells. It seems to have first been suggested by Waldeyer<sup>3</sup> that the egg-membranes are secretions from the follicular epithelium, and that the latter sends prolongations through the pores into

<sup>1</sup> Cunningham, "On the Structure and Development of the Reproductive Elements in *Myxine glutinosa*," 'Quart. Journ. Micr. Sci.,' 1886.

<sup>2</sup> His, W., 'Untersuchungen über d. Ei und d. Eientwickl. bei Knochenfischen,' Leipzig, 1873.

<sup>3</sup> Waldeyer, 'Eierstock und Ei,' Leipzig, 1870.



the interior of the egg. Eimer<sup>1</sup> is quite positive in his statements of having seen prolongations from the follicular cells project into the pores of the zona. This, however, was only observed in the eggs of the ringed snake. Brock<sup>2</sup> again makes mention of similar processes in the ovum of the barbel and that of *Seryanus hepatus*. Finally, the theory of the egg being nourished by means of prolongations from the follicular cells finds a strong supporter in Lindgren.<sup>3</sup> He shows, moreover, that in the egg of the rabbit even follicular cells occasionally travel through the pores of the zona. Some were observed inside it, and others half way out. I myself have not been able to trace any processes from the follicular cells into the ovum, but it seems to me quite probable that such prolongations do exist. At any rate I believe that the ovum receives its raw material as it were through the radial pores from the follicle. It is then assimilated and transformed by the nucleus and the egg nourished in this manner.

Before I proceed to a description of the follicular layer, I must mention another membrane which has been described by some authors, while its existence has been denied by others, I am referring to an extremely delicate membrane covering the yolk internally to the zona radiata. I have seen such a membrane in some cases in the young gurnard's egg (fig. 13, *m. i.*), that is to say, only in sections of hardened specimens, and not in the adult egg. It has been first described by Ransom, who calls it the inner yolk-sac," in distinction to the outer yolk-sac (zona radiata). He also isolated it in *Gasterosteus*. Oellacher did the same in the trout, after treatment with chloride of gold. Allen Thomson, as well as Kölliker, Eimer. Lereboullet, and Aubert, describe an inner delicate membrane.

Although Ovsiannikov saw this layer in *Perca fluviatilis*, he found no trace of it in *Lota vulgaris*, and comes to the conclusion that it is an artificial product.

<sup>1</sup> Eimer, loc. cit.

<sup>2</sup> Brock, loc. cit.

<sup>3</sup> Lindgren, loc. cit.

His, Waldeyer, Brock, and others, deny the existence of an inner membrane.

In theory, the presence of such a membrane would explain much which seems at present very difficult. If it really existed, we would naturally regard the zona as being secreted from it. It would also place the pores of the former into the same category as those occurring in cuticular formations, with which they indeed have much resemblance.

#### IV. THE FOLLICULAR LAYER.

The follicular layer, or granulosa, surrounds the egg-membranes which I have just mentioned. In the next paragraph I shall speak about its development; hence I need only describe its appearance in the ripe intra-ovarian egg.

In the gurnard's egg it consists of a layer of closely-set cells, which has an average thickness of 0.006 mm. Seen from above, the cells present hexagonal outlines with a central nucleus (fig. 16). The egg lies in a stroma of connective tissue.

In the shanny's egg (*Blennius pholis*) the follicle is peculiarly modified (fig. 15, *f.*). The depth of the cells, which in one half of the egg is only about 0.007 mm., gradually increases until it reaches 0.032 mm. at the opposite side. The cells at that side become drawn out and taper towards the surface of the egg. The space between the cells is filled up with interstitial substance (*i. s.*). Another feature about the follicle in this case is that it touches the zona in all parts, except in a circular portion (*c. p.*), where it is not in immediate contact with it. This space is filled with an apparently viscid substance, which no doubt is secreted by the follicular cells.

Similar peculiar modifications of the granulosa have been observed by Eimer and Brock. McLeod<sup>1</sup> likewise mentions a granulosa composed of elongated cells as occurring in *Gobius niger*.

<sup>1</sup> McLeod, "Recherches sur la structure et le développement de l'app. reproduct. femelle des Téléostéens," 'Arch. de Biologie,' vol. ii, 1881.

Although I have never seen prolongations from the follicular cells pass through the zona, as has been described by Eimer and Lindgren, I strongly believe that the follicle forms the most important source for the nourishment of the egg.

Lindgren<sup>1</sup> observed in the mammalian ovum that granulosa cells occasionally travelled into the egg by means of the pores of the zona. Some were seen inside the egg, and others half way out, and prolongations from the follicular cells were frequently traced to the interior. I may mention that nothing of the kind was noticed by me in the eggs of osseous fishes; indeed, the pores of the zona are much too narrow to allow of their being traversed by the follicular cells.

## V. DEVELOPMENT.

On account of my not being able to obtain all the different ovarian stages, I have made no observations on the origin of the egg. Whether the ovum originates from a simple transformation of an epithelial cell, or whether several unite, as in Elasmobranchs, has not been observed. I believe, however, that probably only one cell is concerned in the formation of the egg. This view is held by Brock<sup>2</sup> and Kolessnikov.<sup>3</sup> The former makes the following statement:—"We often find immediately under the epithelium, and frequently in direct communication with it, numerous masses of cells. These masses are seldom utricular—more often they are round or wedge-shaped. The cells show every gradation from epithelial cells to the smallest ova. The whole process lasts only a very short time."

Kolessnikov also mentions that the primary eggs are formed by the growth of some epithelial cells, one cell giving rise to one ovum. A division of the ovum, as described by Waldeyer, could not be found by the same author in either Amphibians or Teleosteans.

<sup>1</sup> Lindgren, loc. cit.

<sup>2</sup> Brock, loc. cit.

<sup>3</sup> Kolessnikov, "Ueber d. Eientwicklung bei Batrachiern und Knochenfischen," 'Arch. f. mikr. Anatomie,' vol. xv, 1878.

The smallest ova I saw were those of *Gadus æglefinus*, which measured only 00·11 mm. in diameter (fig. 1). By far the greater portion of the egg was taken up by the nucleus, and many of the numerous nucleoli were already ranged round the inner surface of the nuclear membrane. A small zone of protoplasm covered the nucleus outside. Apparently there was no cell-membrane. The follicular layer was likewise absent.

In the next larger size, such as we find in fig. 2, which was taken from the gurnard's ovary, we find that the protoplasm surrounding this nucleus is divided into a dark and light zone. The explanation of this peculiar feature was given in Chapter II. Among the nucleoli some are frequently of a very large size. In figures 6 and 7 we now notice a follicular layer surrounding the yolk and bulging somewhat into it, but the cells composing it are large and not numerous. In fact at first a few cells cover the whole of the ovum.

I have not arrived at any definite conclusion as to the origin of the follicular layer. There are three possible ways in which it might have arisen :

1. From outside the egg, by an aggregation of epithelial cells round the ovum, as in Elasmobranchs (Balfour).

2. From outside the egg by connective tissue or endothelial cells collecting at the periphery of the ovum. Teleosteans (His, Ovsianikov). Cephalopoda (Lankester).

3. From inside the egg :

- a. From the vitellus as in Ascidians (Sabatier).

- b. From the nucleus as in Ascidians (Roule, Fol).

Myriapods (Balbiani). Orthoptera (Will).

Although some of my observations seem to show that the follicular epithelium takes its origin from the interior of the egg, others point the opposite way, and, on the whole, I think it would probably be more correct to assign its origin to the connective tissue. At any rate it is ready formed before an egg-membrane can be discovered. Brock can give no opinion as to the origin of the follicle. According to His the very young ova are often surrounded by a double



membrane of endothelium, while there is no trace as yet of a granulosa.

In a young egg (fig. 6), as I mentioned before, a few large flat cells cover its whole surface. As the ovum increases in size they become more numerous and much smaller, until in the ripe eggs they have the appearance as seen in figures 6, 14, 15, *f*.

I have already spoken of the peculiar modification of the follicular layer in *Blennius pholis*, and need not refer to it again.

With regard to the origin of the egg-membranes, it was stated that they appear after the follicle. The first membrane is the zona radiata (figs. 8, 13, 14, 15, *z*). When it is fully developed the inner "zonoid" layer is formed in those eggs in which it is found. In *Blennius pholis* no zonoid layer ever appears. In the gurnard an inner layer was seen in sections of middle-sized eggs, but in later stages no such layer could be discovered. I have had occasion to refer to this layer in a previous paragraph. I myself have no doubt that the egg-membranes originate from the yolk. Ovsiannikov<sup>1</sup>, however, holds that the zona is derived from the follicle; and Cunningham,<sup>2</sup> although he has not had an opportunity of investigating the subject more closely, comes to a similar conclusion.

According to Eimer an outer layer chorion, of which I saw nothing in the ova which I examined, originates from the follicular cells. He, as well as most other authors who have dealt with this subject, agree in the vitelline origin of the zona radiata and the zonoid layer. In the ripe egg the zonoid layer has disappeared completely.

Before concluding this short note on the intra-ovarian egg of osseous fishes, I must refer to a few points which have not been dealt with. An opening appears in the zona radiata before the extrusion of the ovum from the ovary. This "micro-pyle," as it has been called by its discoverer "Doyère," may

<sup>1</sup> Ovsiannikov, loc. cit.

<sup>2</sup> Cunningham, loc. cit.

represent an enlarged canal of the zona, but I have made no direct observation to prove this assertion. According to Cunningham the micropyle in *Myxine glutinosa* is formed by the growth of a cellular process from the follicular epithelium towards the vitelline while the vitelline membrane is being formed.

Another point which has still to be made out, is the ultimate fate of the nucleus and the appearance of a "discus proli-gerus" in the unfertilised egg. I hope, however, to make additional researches at some future period, in order to clear up these matters.

## EXPLANATION OF PLATE V,

Illustrating Dr. R. Scharff's paper "On the Intra-ovarian Egg of some Osseous Fishes."

FIG. 1.—Intra-ovarian ova of *Gadus æglefinus*. (Zeiss D<sup>3</sup>.) *n'*. Nucleoli.

FIG. 2.—Intra-ovarian ovum of *Trigla gurnardus*. (Zeiss D<sup>4</sup>.) *N*. Nucleus. *n'*. Nucleoli.

FIG. 3.—Intra-ovarian ovum of *Trigla gurnardus*. (Zeiss D<sup>4</sup>.) *N*. Nucleus. *n'* Nucleoli. *pr*. Dark protoplasmic ring. *l. p*. Light protoplasm.

FIG. 4.—Nucleus of intra-ovarian ovum of *Hippoglossides limandoides* (Zeiss D<sup>4</sup>.) *n'*. Nucleoli.

FIG. 5.—Intra-ovarian ovum of *Conger vulgaris*. (Zeiss D<sup>3</sup>.) *n'*. Nucleoli.

FIG. 6.—Intra-ovarian ovum of *Gadus virens*. (Zeiss D<sup>4</sup>.) *n'*. Nucleoli. *pr*<sup>1</sup>. External protoplasmic ring. *pr*<sup>2</sup>. Internal protoplasmic ring. *f*. Follicle. *l. p*. Light protoplasm.

FIG. 7.—Intra-ovarian ovum of *Gadus virens*. (Zeiss F<sup>3</sup>.) *n'*. Nucleoli. *n. f*. Nuclear figure. *N. m*. Nuclear membrane. *pr*. Protoplasmic ring. *sp*. Spots (nucleoli?). *f*. Follicle.

FIG. 8.—Intra-ovarian ovum of *Trigla gurnardus*. (Zeiss D<sup>3</sup>.)  
*n.f.* Nuclear figure. *z.* Zona radiata. *zo.* Zonoid layer. *f.* Follicle.

FIG. 9.—Nucleus of intra-ovarian ovum of *Trigla gurnardus*. (Zeiss F<sup>4</sup>.)  
*n'.* Nucleoli. *N<sup>1</sup>.* Old nucleus. *n.f.* Nuclear figure.

FIG. 10.—Yolk-spherules (*Trigla gurnardus*). (Zeiss D<sup>4</sup>.)

FIG. 11.—Yolk-spherules (*Lophius piscatorius*). (Zeiss D<sup>3</sup>.)

FIG. 12.—Nucleus of nearly ripe ovum of *Trigla gurnardus*. (Zeiss D<sup>3</sup>.)  
*N.* Nucleus. *n'.* Nucleoli. *va.* Vacuole.

FIG. 13.—Middle-sized egg of *Trigla gurnardus*. (Zeiss D<sup>3</sup>.) *z.* Zona. *zo.* Zonoid layer. *i.m.* Internal membrane.

FIG. 14.—Intra-ovarian ovum of *Trigla gurnardus* nearly ripe. (Zeiss D<sup>3</sup>.)  
*z.* Zone radiata. *zo.* Zonoid layer. *f.* Follicle. *y.sp.* Yolk-spherules.

FIG. 15.—Intra-ovarian ovum of *Blennius pholis*. (Zeiss D<sup>3</sup>.) *f.* Follicle. *i.s.* Interstitial substance. *c.p.* Circular portion filled with viscid matter. *z.* Zona radiata.

FIG. 16.—Follicular cells of *Trigla gurnardus* (seen from above). (Zeiss D<sup>3</sup>.)

FIG. 17.—Follicular cells of *Blennius pholis* (seen from above). (Zeiss D<sup>3</sup>.)

**Observations on the Structure and Distribution  
of Striped and Unstriped Muscle in the  
Animal Kingdom, and a Theory of Muscular  
Contraction.**

By

**C. F. Marshall, M.Sc.,**

Platt Physiological Scholar in the Owens College, Manchester.

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With Plate VI.

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STRIPED muscle has long been known to occur widely distributed in the animal kingdom, but the details of the structure of the striped muscle-cell have been the subject of much controversy. Various descriptions have been given, widely differing from one another, and none of them affording a satisfactory basis of comparison with other cells. The demonstration of an intracellular network in the muscle-fibre by several recent observers appears to afford the most rational clue to its structure, for it not only explains all the appearances seen in the muscle-fibre, including those seen with polarised light in the living fibre by Brücke, but it also renders possible a comparison with other cells, and shows that a muscle-fibre is to be regarded as of essentially the same structure as an ordinary cell, and must not be considered as an enigmatical structure, the details of which do not correspond to those of any other cell in the animal economy.

It is necessary first to examine the descriptions of the several observers who have described a network in the striped muscle-fibre and to consider the interpretation that they have put upon it. In the following account I have only referred to those



observers who have described some form of network in the muscle-fibre.

Dr. G. Thin<sup>1</sup> appears to be the first observer who described an intracellular network in the fibre of striped muscle. He examined frog's muscle treated with gold chloride in the following manner. After staining with gold chloride the muscle was exposed to light in acidulated water and then kept in strong acetic acid, at a temp. of 38° C., from 6—24 hours. By this method he demonstrated a network of fine fibres, concerning which he says "this network was composed of exceedingly fine fibres, and its meshes accurately corresponded to Cohnheim's areas" (p. 252). He states that he demonstrated in the muscle-fibre, by the process of isolation, (1) the existence of flat cells (the muscle-corpuscles), (2) a network connected with central cellular protoplasm, and (3) parallel rows of spindle elements. Further on he states that he was "compelled to associate the transverse markings with the existence of this network, without attempting to explain the connection between them more definitely" (p. 258).

Gerlach<sup>2</sup> has written two papers on this subject. In the first paper he states that the contractile contents of the sarcolemma is traversed by a retiform substance continuous with and identical with the axis cylinder of the nerve. He thus regards the network as of a nervous nature.

In the second paper he states that (i) an intravaginal nerve network is present within the sarcolemma. (ii) In good specimens striæ are seen which behave in a similar manner to the intravaginal network, and can be traced into continuity with it. He divides muscle into an anisotropic contractile matrix, and an isotropic nerve network. His results were obtained by the following method: the gold preparations were left several days in a mixture of 1—2 parts hydrochloric acid,

<sup>1</sup> "On the Structure of Muscular Fibre," 'Quart. Journ. Micr. Sci.,' vol. xvi (N. S.), 1876, pp. 251—259.

<sup>2</sup> 'Das Verhältniss der Nerven zu den Muskeln der Wirbelthiere,' Leipzig (Vogel), 1874. "Ueber das Verhältniss der nervösen und contractilen Substanz der quergestreiften Muskeln," 'Arch. f. Mik. Anat.,' Bd. xiii, 1877, p. 399.

20 parts glycerine, and 20 parts water. This method brought out the longitudinal striæ. On treating gold preparations as above and subsequently treating with 1 per cent. potassium cyanide, he states that the sarcolemma gives way and the contents escape, partly as fine particles and partly in larger pieces; in such pieces the transparent substance bounding Cohnheim's areas was stained red, and was thickened at the nodal points. The muscle-corpuscles always lay in the stained substance and not in Cohnheim's areas; they consisted of a central oval nucleus and a stained peripheral substance continuous with the stained network of longitudinal striæ. He states that the longitudinal striæ are very variable in thickness and always zigzag; never straight. He regards them as thickenings of fine sheaths of nervous matter enclosing the fibrillæ of the muscle; these sheaths corresponding to the boundaries of Cohnheim areas.

He therefore concludes that the intravaginal nerve plexus and the longitudinal striæ are continuous, and together make up the isotropous part of the muscle-fibre, and are to be considered as nervous. To them belong also the muscle-corpuscles and the nuclei of the intravaginal nerves. He regards the anisotropous matrix as the contractile part. Gerlach thus appears to view the isotropous part of the muscle, stained by the gold, as a honeycomb and not a true network of fibrils. He has apparently failed to observe the transverse networks, and does not attempt to explain the relation between the network and the transverse striation.

The existence of an intravaginal nerve plexus in the muscle-fibre, and also the continuity of the nerve end plate with the isotropous part of the muscle, have been denied by Ewald<sup>1</sup> and Fischer.<sup>2</sup>

Engelmann<sup>3</sup> regarded the isotropous part of the fibre as a structure "das in Physiologisches Hinsicht von einem Nerven nicht wesentlich abweichen Wunde," and suspected a connection with the axis cylinder.

<sup>1</sup> 'Arch. für Mikr. Anat.,' Bd. xiii, pp. 365—390.

<sup>2</sup> 'Pflüger's Archiv,' Bd. xii, pp. 529—548.

<sup>3</sup> 'Pflüger's Archiv,' Bd. xi, p. 462.

In a later paper Engelmann<sup>1</sup> states that the contractility of the muscle-fibre is always connected with fibrillar elements in the fibre; and he compares these with fibrillar elements in the protoplasm of some of the Rhizopods and Infusoria, &c.

Retzius<sup>2</sup> describes very carefully a network in the muscle-fibre of *Dytiscus* and other forms. This network consisted of (i) transverse networks placed at regular intervals, and corresponding in position to Krause's membranes. (ii) Longitudinal bars parallel to each other, and apparently running the whole length of the muscle-fibre, and connected with the transverse networks. His results were obtained partly by transverse and longitudinal sections, and partly by teased preparations. He also employed the following method of gold staining: the specimens were placed for twenty-five minutes in  $\frac{1}{5}$ — $\frac{1}{2}$  per cent. gold chloride, either with or without previous immersion in 1 per cent. formic acid; then in 1 per cent. formic acid for ten to twenty hours, and exposed to the light. He gives the following description of the muscle-fibre of *Dytiscus*: In the axis of the fibre there are one or more rows of muscle-corpuscles, the protoplasm of which is produced into several (2—5) processes from which finer processes arise forming the transverse networks. Each muscle-corpuscle is in connection with five or six successive transverse networks. The longitudinal bars of the network he describes rather doubtfully as consisting of rows of dots (p. 8), but he describes and figures them projecting freely in some preparations. The matrix is structureless, and is only slightly stained by the gold. The sarcolemma is apparently closely attached to, but probably independent of, the network. The nerve endings appear to be in close connection with the transverse networks. The function of the network he was unable to determine, but states that it is probably not merely a supporting framework, but actively concerned in contraction. He does not, however, regard it as the true contractile part,

<sup>1</sup> 'Pflüger's Archiv,' Bd. xxv, 1881, pp. 538—565.

<sup>2</sup> "Zur Kenntniss der quergestreiften Muskelfaser," 'Biologische Untersuchungen,' 1881, pp. 1—26, Pls. i, ii.

as, according to him, it does not undergo important changes in form during contraction and extension. He thinks that the network is probably concerned in conveying the stimulus from the nerve to the muscle-fibre. In support of this he mentions that the fibre, as a rule, contracts simultaneously throughout its whole thickness; also that the nerve-fibres are apparently connected with the transverse networks.

Retzius also examined muscle from *Musca*, *Oestrus*, *Notonecta*, *Locusta*, *Astacus*, *Rana*, and *Triton*. In *Locusta* the transverse networks had more polygonal meshes than in *Dytiscus*. In *Astacus*, *Rana*, and *Triton* the longitudinal bars of the network were thicker than the transverse.

In some cases he states that the longitudinal bars of the network were not straight but zigzag. From the descriptions and figures it is very probable that this appearance was due to pressure, and is not normal.

Bremer<sup>1</sup> also describes a well-defined network in the striped muscle-fibre, evidently identical with that described by Retzius. He states that the longitudinal lines are true fibrils, and not part of cylindrical sheaths as Gerlach maintained. He further traces the axis cylinder of the nerve into direct continuity with the muscle-corpuscles.

He considers the longitudinal striæ of Gerlach to be identical with the longitudinal bars of the network, and explains the irregular dotted appearance, or "Sprenkelung," of Gerlach's longitudinal striæ as being due to imperfect staining.

Bremer's results, though published subsequently to those of Retzius, were obtained quite independently.

B. Melland<sup>2</sup> has recently investigated the structure of the striped muscle-fibre, and has arrived independently at results agreeing very closely with those of Retzius and Bremer. This close correspondence between the accounts of these three

<sup>1</sup> 'Arch. für Mikr. Anat.,' Bd. xxii, 1883, pp. 318—356.

<sup>2</sup> "A Simplified View of the Structure of the Striped Muscle-fibre," 'Quart. Journ. Micr. Sci.,' July, 1885.



observers affords satisfactory evidence of the correctness of their observations.

The points of difference between the networks described by Melland and Retzius are slight, the chief one being that Melland figures the transverse networks in *Dytiscus* with more polygonal meshes, and furnished with nodal thickenings at the points of junction with the longitudinal bars of the network. Retzius figures these in *Locusta*, but in *Dytiscus* he describes the transverse networks as generally composed almost entirely of radial fibres with very few transverse connections; and in place of nodal dots he describes several thickenings or nodes placed irregularly, and much fewer in number than the nodal dots described by Melland. Melland does not trace any connection between the network and the muscle-corpuscles nor with the nerve endings. He shows how the optical appearances of striped muscle are caused by the network. He considers the network to be intimately connected with the sarcolemma, and to be homologous with the intracellular networks which have been described in other cells. It is evident from fig. 6 of his paper that we have to do with a true network and not a honeycomb, a fact which is not so apparent from the figures of Retzius and Bremer. I have reproduced the figure from Mr. Melland's paper (fig. 18).

Mr. Melland's results were obtained partly in conjunction with myself, and the object of the present paper is a continuation of this investigation. I have endeavoured to trace the distribution of this intracellular network of the striped muscle-fibre in the animal kingdom, and also, so far as possible, to determine its function.

The striation of muscle must not be confounded with a transversely striated appearance caused by a corrugated outline of the fibre, possibly due to a state of over-contraction. Such a false striation is met with occasionally in some fibres in the *Echinus*, *Leech*, &c., and is the cause of the muscles of these animals having been described as striped. I shall, therefore, only describe muscle as being striped when the striation is

due to the presence of the intracellular network, described by Retzius, Bremer, and Melland.

I have examined muscle taken from representatives of the chief groups of the animal kingdom with the special object of investigating the presence of an intracellular network in the muscle-cells, either such as that of the striped muscle-fibre, or, when this does not exist, an intracellular network of any kind.

The *Amœba* and *Hydra* have been included in this investigation; for it is an important point to determine the existence of an intracellular network in such a primitive and eminently contractile cell as the *Amœba*; it is also important to investigate the structure of the muscular processes of the ectoderm cells of the *Hydra*, as they are supposed to represent the first beginning of a muscle-cell.

In all cases the outlines and main details of the figures were drawn with the camera; in most cases under the  $\frac{1}{10}$ th immersion objective of Beck with No. 2 eyepiece, giving a magnifying power of 1100 diameters.

**Methods of Preparation.**—The chief method of preparation used was the method of gold staining employed by Melland. The gold stains and renders evident the intracellular network of most cells, especially the network of the striped muscle-cell; hence it is at once a test whether the striation of the fibre is due to the presence of the network, or whether it is merely the false striation mentioned above.

Various modifications of the gold method were employed according to the delicacy of the tissue under investigation. The method employed by Melland consists in placing the muscle in 1 per cent. acetic acid for a few seconds; then in 1 per cent. gold chloride for thirty minutes; then in formic acid, 25 per cent., for twenty-four or forty-eight hours in the dark.

This answers well for vertebrate and insect muscles. But for the more delicate organisms, such as the *Hydra*, *Daphnia*, &c., and the heart muscle of invertebrates, I found a one hour's immersion in formic acid, exposed to strong sunlight,

to be the best treatment; or, in some cases, a warm chamber (40° C.) was used. A longer immersion than one or two hours in the formic acid in these cases leads to disintegration of the tissues. In addition to the gold preparations, osmic acid preparations were made in most cases, and compared with those made by the gold method. Osmic acid is well known for its property of fixing the histological elements in their natural state.

The examination of fresh tissues was in many cases of very little use; for the cells of the striped muscle of many of the animals investigated are so small that under a high power they barely appear striped, and no network can be seen at all. In these cases it is only by softening the fibre and so swelling it out, and at the same time staining the network, that the latter can be demonstrated; this is the special action of the method of gold staining.

It is necessary to mention that the results obtained by the gold method are somewhat uncertain. In some cases the network will come out distinctly, but in others, especially when the preparation has been left for a longer time than usual in the acetic acid, the network appears to consist of rows of granules instead of definite lines. This uncertainty was noticed also by Retzius, Gerlach, and Bremer, and is no doubt the cause of the different appearances described by these authors.

In order to avoid the monotony and interruption of repeatedly stating the treatment used for the muscle of each animal, the exact method used is given with the description of the figure of each animal in the plates at the end of the paper.

I shall now take the chief group of the animal kingdom in their zoological order, describing the muscle found in each case.

## STRUCTURE AND DISTRIBUTION OF MUSCLE IN THE ANIMAL KINGDOM.

### PROTOZOA.

*Amœba*.—Klein<sup>1</sup> states, on Heitzmann's authority, that under suitable conditions the protoplasm of the white blood-corpuscles can be seen to contain an intracellular network composed of fine fibrils. Dr. Klein has, however, recently informed me that he does not find an intracellular network in the *Amœba*, nor in the majority of white blood-corpuscles.

On examination of very large specimens of *Amœba princeps* in the fresh state the constant flowing movement of the protoplasm renders it difficult to conceive of any permanent intracellular network. I have, moreover, made gold preparations of these *Amœbæ* in the following manner:—The *Amœba* was placed in a drop of water with a little cotton wool underneath the cover glass to prevent the animal being washed away by the reagents. A few drops of 1 per cent. acetic acid were then run in under the cover glass for a few seconds. Gold chloride was then run in, and the animal left in this for fifteen minutes. Formic acid was then added, and the animal left exposed to light for about one hour; by this time the gold was reduced and the animal stained. The preparation was then mounted in dilute glycerine.

*Amœbæ* prepared in this way showed no trace of an intracellular network; the protoplasm simply presenting a mottled granular appearance.

Although there is no definite intracellular network, comparable to that of an ordinary epithelial or gland cell, known to exist in any of the Protozoa, yet a vacuolated condition of the protoplasm is well known to occur in many of them. This attains a high degree of development in many forms, e. g. *Noctiluca*. These vacuoles are certainly not all food vacuoles, and may possibly indicate the starting point of the differentiation of an intracellular network, i. e. a differentiation of the cell into

<sup>1</sup> 'Atlas of Histology,' p. 2, diag. 1.



firmer and less dense parts, the former of which takes on the form of a network or reticulum. For although it is not absolutely certain that the structures described as intracellular and intranuclear networks are in all cases denser than the rest of the protoplasm of the cell, they are, I believe, generally assumed by histologists to be so, and also to be protoplasmic in nature.

#### VORTICELLA.

The stalk of the Vorticella contains a spiral protoplasmic fibre, which is eminently contractile. This fibre, when treated with the gold staining, shows no trace of the presence of fibrils, having simply the appearance of undifferentiated protoplasm.

#### CÆLENTERATA.

Hydra.—The peculiar ectoderm cells of the Hydra are important to investigate, since they are generally held to represent the first commencement of a muscle. Here the one cell is differentiated into two parts to perform two functions, the one portion to act as a sensory cell, the other to act as a muscle.

Hamann<sup>1</sup> describes, in the epithelial muscle-cells of the hydroid polypes, a network in the body of the cell, but in fibrillation in the muscular process.

My own observations on the cells of the Hydra agree with those of Hamann. Gold preparations of these cells show a network in the body of the cell, but no continuation of it into the muscular process (fig. 1).

Medusa.—Striated muscle has been described as occurring in the disc of Aurelia by Max Schultze, Brücke, and Virchow, and in Pelagia by Kölliker.<sup>2</sup>

In gold preparations of muscle from the disc of Aurelia I find distinct transverse striation, which, under the  $\frac{1}{10}$  immersion objective, is found to be due to the presence of a network

<sup>1</sup> 'Organismus der Hydroid Polypen,' p. 15.

<sup>2</sup> 'Stricker's Handbook of Histology,' vol. iii, p. 551.

similar, in all respects, to the network described by Retzius and Melland in striped muscle (fig. 2).

*Actinia*.—Muscle taken from the base of the *Actinia* and treated with gold was found to consist of elongated fusiform cells, non-striped, and showing no trace of any intracellular network, or of any fibrillation.

Hence the conclusions obtained are that in the muscular process of the *Hydra* cell there is no form of network or fibrillation, although a network is present in the body of the cell. In the more highly organised *Medusa* the typical network of striped muscle is found to be present, but in the equally highly organised *Actinia* no network is present, nor is there any fibrillation in the muscle-cells.

These results agree with those obtained by Hamann<sup>1</sup> by the method of isolating the cells by maceration in various reagents. He states that the muscles of *Hydroid* polypes are always smooth, and quite distinct from the striated muscles of the *Medusæ*. Hamann thinks that where transverse striation has been described in *Hydroid* polypes it is probably due to the action of reagents.

The Hertwigs,<sup>2</sup> in their observations on the *Actiniæ*, describe no fibrillation in the muscle-fibre. They investigated the tissues of *Sagartia* and *Anthea*.

#### ECHINODERMATA.

The muscle of the *Echinoderms* has been described as striped by several observers. Firstly, by Schwalbe<sup>3</sup> in the muscle-cells between the ambulacral plates of *Ophiothrix*, and more recently by Geddes and Beddard.<sup>4</sup> From the figure given by the latter observers it is evident that the striation they describe is the false striation mentioned above as being due to annular constrictions. Schwalbe, however, describes double oblique striation.

<sup>1</sup> Loc. cit., p. 20.

<sup>2</sup> 'Die Actinien.'

<sup>3</sup> 'Archiv für Mic. Anat.,' 1869, p. 205.

<sup>4</sup> 'Proc. Royal Soc. Edinburgh,' 1873.

I have made gold preparations of muscle taken from the "lantern of Aristotle" of *Echinus*, and find no trace of the network of striped muscle or of any fibrillation. The cells are remarkable for the clearness and transparency of their protoplasm.

These results again agree closely with those obtained by Hermann.<sup>1</sup> He describes the muscle of the Asterids as smooth, and very seldom showing fine longitudinal fibrillation. In the Holothurians he describes the muscle as non-striped, but states that longitudinal fibrillation is to be seen in it.

#### VERMES.

*Hirudo*.—The muscle-fibres of the Leech are peculiar: they consist of an outer clear portion and a central granular part. In gold preparations the outer part stains the more deeply of the two portions of the cell and appears quite homogeneous, showing no trace of a network. In osmic acid preparations the outer layer appears very faintly fibrillated, but I could not identify any distinct fibrils differentiated from the rest of the cell even under the  $\frac{1}{10}$  immersion objective.

Transverse sections of the muscle of the Leech show a radiating appearance of dark and light bands in the outer portion of the cell. This is, I believe, caused by the method of preparation, for in some sections the outer portion of the cell is broken up into pieces arranged in a radiating manner and corresponding to the light portions between the radiating dark lines in the better preserved specimens. I find nothing corresponding to this appearance in muscle prepared by the gold or osmic acid methods, which are the methods generally recognised as maintaining the true histological characters of cells intact.

Wagener,<sup>2</sup> from transverse sections of dried specimens of Leech, states that the muscle-cells consist of a central medul-

<sup>1</sup> 'Asteriden,' p. 94, plate iii; 'Holothuranien,' p. 38, plate ii.

<sup>2</sup> 'Archiv f. Mic. Anat.,' 1869.

lary substance round the nucleus, and a cortical substance splitting into fibrils. This is also described by Schwalbe<sup>1</sup> in the fibres of *Aulostoma*.

*Lumbricus terrestris*.—Gold preparations of the muscle of the Earthworm show large elongated cells which on close examination show longitudinal lines; these under the  $\frac{1}{10}$  immersion objective present a dotted appearance (fig. 3). At first sight it might appear that we have here the network of striped muscle; but this is not the case. In the first place, there is no appearance of transverse striation at all; in the second place, the dots are not arranged transversely but are quite irregular; lastly, so far as I could observe, the dotted lines are superficial and do not extend into the body of the cell.

One of the so-called "hearts" of the worm was treated in the same way; the muscle-cells were found to resemble almost exactly the muscle-cells described above.

In the Polyzoa and Rotifera striped muscle is well known to occur. I have not, however, been able to determine with certainty whether the striation is due to the presence of a network or not. Nitsche<sup>1</sup> says that the striation in the retractor muscle of the Polyzoa is not due to any wrinkling of the sarcolemma. The retractor muscle appears to be the only muscle that is striped from Nitsche's observations.

Striped muscle has been recently described by Haswell<sup>2</sup> in the gizzard of *Syllis* one of the Polychæte worms.

## MOLLUSCA.

According to Schwalbe,<sup>3</sup> double oblique striated muscle is present in *Solen*, *Ostrea*, and *Helix*.

*Anodon*.—Preparations of the adductor muscle of the *Anodon* treated with gold show that the muscle consists of small elongated cells of the unstriped type, showing no fibrillation

<sup>1</sup> 'Kenntniss der Bryozoen,' Heft 2, p. 55.

<sup>2</sup> 'Quart. Journ. Mic. Sci.,' 1886.

<sup>3</sup> 'Arch. f. Mic. Anat.,' 1869.



or transverse striation. The muscle treated with osmic acid shows faint fibrillation, but no distinct fibrils.

*Patella*.—The Limpet was chosen for an investigation of the structure of the heart muscle. In gold preparations of the ventricle I find the network of striped muscle present (fig. 5).

In the heart of the *Anodon* I could not determine with certainty whether the network was present or not, although faint indications of it were obtained.

*Ostrea*.—The adductor muscle of the Oyster consists of two portions: a white opaque portion, and a more gelatinous portion. Gold preparations were made of each of these. The cells of the "white muscle" are large, with clear outlines, and remarkable for the clearness and transparency of their protoplasm. The cells of the "gelatinous muscle" are smaller and less transparent. Neither of these showed any network or fibrillation.

*Helix pomatia*.—Gold preparations of the muscle of the foot show that it consists of very small cells of the unstriped type densely massed together.

The muscle of the odontophore, however, shows transverse striation, which under the high power is seen to be caused by the presence of the typical network of striped muscle.

*Pecten*.—The *Pecten* differs from most of its class by performing rapid movements of its adductor muscle whereby it propels itself through the water. Gold preparations of the adductor muscle made by my friend Mr. J. T. Cunningham show the network of striped muscle very plainly (fig. 4). I have not observed the double oblique striation described by Schwalbe in the muscle of Molluscs and Echinoderms. As this is not seen in gold and osmic acid preparations, I think it must be an optical effect. Schwalbe, indeed, admits that in *Ophiothrix* the transverse striation is due to folds in the sarcolemma (loc. cit., p. 211).

## ARTHROPODA.

Representatives of the Crustacea and Insecta, viz. the Lobster, Dysticus, and the Bee, were investigated by Mr. Melland,<sup>1</sup> the network (of striped muscle) being found in each case.

*Astacus*, Heart-muscle.—Gold preparations of the heart of the Crayfish show the network to be present in this muscle as in the body muscles; the network is, however, much finer and more difficult to demonstrate (fig. 6).

The muscle-fibres of the heart are intimately blended with what appear to be large masses of granular protoplasm enclosing nerve-cells; these may possibly be of the nature of nerve-endings.

*Daphnia*.—As a representative of the minuter forms of Crustacea, I examined the *Daphnia*. The muscle-fibres of this animal, when examined in the fresh state, only show transverse striation faintly. After many attempts I succeeded in obtaining a satisfactory gold preparation, where the muscle-fibres were much softened and pressed out to many times their normal diameter. These fibres show the network very plainly (fig. 7).

In this case the animal was placed whole in 1 per cent. acetic acid for ten minutes, and left in the formic acid in a warm chamber at 40° C. for two hours.

*Insect Larva*.—To determine if striped muscle is present in the larval insect as well as in the imago, I made preparations from the larva of the Ermine Moth (*Spilosoma lubricipeda*). Muscle was taken both from the jaws and from the legs. In both cases the muscle was found to be striped, the network in the muscle of the jaw being especially well developed.

## ARACHNIDA.

Muscle taken from the leg of the Spider and treated with gold showed the network of striped muscle.

<sup>1</sup> Loc. cit.

## VERTEBRATA.

The vertebrate animals examined by Mr. Melland were the Frog and the Rat. These will serve as examples of the Amphibia and Mammalia. I have examined the muscle of animals taken from the other chief groups, viz. the Cyclostomata, Elasmobranchia, Teleostea, Reptilia, and Aves, taking as representatives of these groups respectively: Myxine, Scyllium, Gasterosteus, Testudo, and Turdus.

Muscle taken from each of these animals was treated with the usual gold method, and in each case a network was found identical with that described by Melland. On comparing these networks with one another and with those described above in the striped muscle of the several invertebrate animals, they are found to agree in all respects.

With regard to *Amphioxus*, I have not had the opportunity of examining fresh specimens. The muscle has, however, been described as striped,<sup>1</sup> and (from analogy) I see no reason to think that the striation is due to any other cause than a network. In the Ascidian, I have examined the muscular bands of *Salpa* and find striped muscle present.

## CARDIAC MUSCLE.

The heart muscle has long been described as faintly striped transversely, but whether this striation is due to the same cause as that to which ordinary striped muscle owes its striation, has not been determined with certainty.

In order to investigate this point, I made gold preparations of muscle taken from the Rat's heart. The cells are seen to contain a network similar to that of ordinary striped muscle. The network is more delicate and with much smaller meshes than the network in the body muscle of the same animal, and is therefore more difficult to demonstrate by the gold method (fig. 9). I have also prepared muscle from the heart of the

<sup>1</sup> Grenacher, 'Zeit. für wiss. Zool.,' p. 577.

Frog (fig. 10) and Bird (fig. 11); the network in the latter animal is much plainer than in the others.

The striation of cardiac muscle therefore appears due to an intracellular network similar to that of ordinary striped muscle.

#### UNSTRIPED MUSCLE OF VERTEBRATES.

Klein<sup>1</sup> describes in the unstriped muscle of vertebrates a bundle of longitudinal fibrils which are in connection with the intranuclear network. This description of the structure of the unstriped muscle-cell is as follows: "Thus we may regard the unstriped muscle-fibre as composed of a sheath with annular thickenings and a bundle of delicate fibrils which at one more or less central point forms a delicate network. This, surrounded by a special membrane—except where the network is in connection with the bundle of fibrils—represents the nucleus." Klein regards the bundle of fibrils as the contractile part of the cell, and thinks that by their shortening the muscle-fibre is caused to contract, elongation being produced by the elastic rebound of the sheath. Flemming<sup>2</sup> has observed these fibrils in the living muscle.

Dr. Klein informs me that he regards the bundle of longitudinal fibrils as representing an intracellular network homologous with other intracellular networks. Dr. Klein has been kind enough to show me his preparations of unstriped muscle prepared from the mesentery of the newt by twenty-four hours immersion in 5 per cent. ammonium bichromate, and afterwards stained with logwood. These preparations show clearly the longitudinal fibrils and their connection with the intranuclear network.

I have made preparations, by the gold method, of muscle from the mesentery of the newt and from the bladder of the

<sup>1</sup> Klein, 'Atlas of Histology,' p. 74, pl. xv; also 'Quart. Journ. Micr. Sci.,' 1878.

<sup>2</sup> "Beobachtungen über die Beschaffenheit des Zell Kerns," 'Arch. für Mikr. Anat.,' 1876, Bd. xiii, pp. 714, 715.



Salamander, in both of these the fibrils in the muscle-cells are very evident, but the intranuclear networks do not show at all distinctly, which is a most unusual result in this mode of preparation. However, in preparations from the mesentery of the newt, made by Klein's method, the intranuclear networks come out very distinctly in many fibres; and in one case I could trace the connection of the intranuclear network with the fibrils of the cell. The longitudinal fibrils do not show so well in these preparations as in those made by the gold method (figs. 12, 13). It thus appears that the vertebrate unstriped muscle differs from all the invertebrate unstriped muscle that I have investigated, in that the cells contain an intracellular network in the form of longitudinal fibrils. This may perhaps represent a form of network intermediate between the typical irregular network of other cells and the highly modified network of the striped muscle-cell.

From these investigations it appears that the peculiar intracellular network of striped muscle is developed in all muscles which have to perform rapid or regular movements.

A brief review of the chief animals mentioned in the preceding pages will make this clear. Commencing with the *Actinia* and the *Medusa*, these are both highly organised Coelenterates, but the *Actinia* is a sluggish animal which exhibits slow and irregular movements, while the *Medusa* propels itself through the water by rapid and regular contractions of its disc. Now, in the *Actinia* we find no striped muscle, but in the *Medusa* the network is present. In the worms such as the *Leech* and *Earthworm* striped muscle is absent; these animals only performing comparatively sluggish movements. In the *Polyzoa* the retractor muscles of the stomach, and in the *Rotifers* the retractors of the trochal disc, perform rapid movements, and have been described as striated transversely; this is probably due to the network, although, as stated above, I have so far been unable to determine this myself. In the *Mollusca* the movements are as a rule sluggish, and unstriped muscle is the prevailing type in this group. But in the odontophore muscles of the *Snails* the

movements are more rapid, and in these we find the network developed. Also in the hearts of these animals which perform rapid and regular contractions I find the network present, at any rate in the case of *Patella*.

In the *Pecten* we have a Mollusc which differs from the majority of its class by performing rapid movements by the contraction of its adductor muscle, and here we find the network present. This is a most important fact in favour of the view that the peculiar network of striped muscle is developed when rapid movements are to be performed; for here we have the *Mussel* and the *Pecten*, both belonging to the same division of the *Mollusca*, and both having adductor muscles moving the valves of the shell. In the *Mussel* the adductor muscles only act at irregular intervals and comparatively slowly; but in the *Pecten* they perform rapid and frequent contractions when the animal swims. In the *Mussel* we find unstriped muscle, but in the *Pecten* the network of striped muscle is present.

In the majority of *Arthropods* and *Vertebrates* the movements are chiefly rapid and of frequent occurrence, and in these groups there is a wide distribution of striped muscle.

It is quite possible that in some animals of sluggish habits, such as some adult insects, the presence of striped muscle may be due to inheritance.

We should expect on this view to find striped muscle present in all well-developed hearts, since they execute rapid and regular contractions. However, in the so-called "hearts" of the *Earthworm* the muscle is unstriped. This can, I think, be explained as follows. These so-called "hearts" represent the earliest and most primitive form of heart in the animal kingdom, being simply local hypertrophies of the blood-vessels which perform rhythmic contraction. Now, the muscle of the blood-vessels is unstriped, therefore we should scarcely expect to find striped muscle in what are simply local hypertrophies of those vessels. Moreover, the contraction of these "hearts" is slow and peristaltic in nature. It is only when we come to the more highly developed hearts, such as those of the *Patella*,

Snail, &c., which have to perform much more rapid and regular contractions than the "hearts" of the worm that we find striped muscle developed.

I may here state that I have not yet been able to determine the nature of the connection between the network of striped muscle and the nerve end-plate, which must exist if the combined results of Retzius and Bremer are correct. This I hope to do in a subsequent paper. I have, however, recently observed the connection between the network and the muscle-corpuscles described by Retzius.

#### THEORY OF MUSCULAR CONTRACTION.

The general conclusions arrived at in the preceding part of the paper are as follows :

(1) An intracellular network of a definite character is present in the fibre of striped muscle throughout the animal kingdom.

(2) This network is developed where rapid and frequent movements have to be performed.

(3) The striped muscle-fibre consists of sarcolemma, network, and sarcous substance ; and, so far as at present determined, there is no other structure present in the fibre (excepting the muscle-corpuscles and nerve-endings).

The question now before us is to determine if possible the nature and function of the network, and what relation it bears to the contractility of the muscle-fibre.

Changes in the Network during contraction.—In order to investigate this point I teased out some perfectly fresh muscle from the leg of a *Dytiscus* and placed it on an inverted cover-glass over a gas-chamber. Alcohol vapour was then blown over the preparation when most of the fibres contracted owing to the chemical stimulus. The vapour was passed over the muscle for about a quarter or half a minute. The fibres were then fixed in their contracted state by plunging them into 5 per cent. acetic acid for half a minute, and then treated with

gold and formic acid in the usual way. Many fibres were thus obtained completely contracted and also many fixed waves of contraction.

I also made preparations of relaxed muscle from a *Dytiscus* killed with chloroform. However, as the fibres vary so much in appearance according as they are more or less pressed out in the gold preparation, comparisons of the muscle stimulated with alcohol vapour, with that reduced by chloroform, though they may give the general effect of the difference, are not absolutely trustworthy. The only way of really proving this point is to examine a fibre, one portion of which is in the relaxed condition and the other contracted, or, in other words, a fixed wave of contraction.

On careful examination of the network in one of these fixed waves of contraction with the  $\frac{1}{10}$  immersion objective the longitudinal fibrils of the network were always straight in all parts of the fibre and appeared slightly thicker in the contracted part of the fibre although it was difficult to judge accurately of the difference in thickness. The nodal dots, however, were the same size in both the contracted and relaxed portions of the fibre. The dots appeared in many cases even smaller in the contracted than in the relaxed muscle. This is, I believe, due to their being more separated from each other laterally, whereby the refractive effects which somewhat obscure the real size of the dots in the relaxed muscle are diminished (fig. 14).

It therefore appears from gold preparations that during contraction the nodal dots do not alter in size but that the longitudinal bars of the network increase in thickness. The apparent enlargement of the nodal dots when the fibre is seen in the fresh state is due to optical effect. Moreover, if the nodal dots do not alter in size it follows necessarily that the longitudinal bars must increase in thickness; for since they keep straight during contraction if they do not increase in thickness there must be a diminution in the volume of the fibre, which is known not to occur.

These results differ from the account given by Schäfer of the



changes during contraction. He states<sup>1</sup> from observations on the living fibre that during contraction his "muscle-rods" (which correspond to the longitudinal bars of the network) become compressed in the centre and their substance tends to accumulate towards the ends, *i. e.* that the knotted ends of the muscle-rods, which correspond to the nodal points of the network, increase in size at the expense of the shafts connecting them. On examination of the living fibre this certainly appears to be the case, but the optical effects of reflection and refraction are so great as to obscure the real change that takes place.

#### NATURE AND FUNCTION OF THE NETWORK.

In discussing the theory of contraction, I shall assume that the intracellular network of striped muscle, and the longitudinal fibrils of the vertebrate unstriped muscle, are of the same nature as other intracellular networks; and, in accordance with the views of modern histologists, that they are protoplasmic in nature, and denser than the rest of the cell.

We have first to consider the nature of intracellular networks in general, and whether the function is an active or a passive one. In the case of intranuclear networks the changes which the network undergoes in karyokinetic division of the nucleus point to their being of an active nature. The extranuclear network (intracellular) is apparently of the same nature as the intranuclear, since the two have been shown to be continuous in many cells; and also they have the same behaviour towards stains and reagents. Moreover, if intracellular networks are developed by a process of vacuolation of the protoplasm of the cell, or a division into denser and less dense parts, as described previously when treating of the Protozoa, it is obvious that in these cases the network must be the active and the contractile part of the cell.

<sup>1</sup> "On the Leg-muscles of the Water-beetle," 'Phil. Trans.,' 1873.

The continuity and identity of nuclear and extranuclear networks is strongly supported by Sedgwick's remarkable observations on the early stages of *Peripatus*.<sup>1</sup> He not only demonstrates the continuity of the extranuclear and intranuclear networks, but he also shows that during segmentation of the ovum the cells do not become completely separated, but remain connected by their protoplasmic networks, i. e. that the intracellular networks of all the cells are continuous.

He also states that the so-called nuclear membrane is reticular in nature and not a true membrane, being, in fact, part of the general reticulum of the cell. In the cells described by Sedgwick there is no doubt that the reticulum is the active portion of the cell, for the rest of the cell consists simply of vacuoles.

Flemming states,<sup>2</sup> as Sedgwick also noticed, that the first change observable in a cell whose nucleus is about to divide is in the extranuclear protoplasm. Strasburger<sup>3</sup> further states that the fibrils which form the nuclear spindle originate in the surrounding "cytoplasm" at the time of division. This appears to be direct evidence of an active function in the intracellular network.

These considerations show that the function of intracellular networks is very probably of an active nature.

We have now to consider the networks of striped and unstriped muscle. Both these forms of network are non-essential to contraction, for we have seen that many muscle-fibres of invertebrates are devoid of a network of any kind; but that they modify the nature of the contraction is very probable.

We have seen that the network of striped muscle is developed when rapid movements are to be performed; this shows that the function of contraction is intimately associated with the presence of the network.

The chief points of difference in the contraction of striped

<sup>1</sup> 'Quart. Journ. Micr. Sci.,' vol. xxvi, 1886, pp. 175—212.

<sup>2</sup> 'Zellsubstanz, Kern u. Zelltheilung,' Leipzig, 1882.

<sup>3</sup> 'Arch. f. Mikr. Anat.,' Bd. xxiii, "Die Controversen der indirecten Kerntheilung."

and unstriped muscle respectively are the great length of the latent period and the long duration of the contraction in the unstriped muscle. The velocity of the contraction-wave in striped muscle is in the Frog, 3—4 metres per second, while in the unstriped muscle (ureter) the velocity is only 20—30 mm. per second.<sup>1</sup> This seems to indicate that the peculiarly arranged network of striped muscle may be associated with the rapidity of its contraction.

In nearly all the specimens I have examined both the transverse and longitudinal bars of the network remain perfectly straight in all conditions of contraction and relaxation of the muscle. Hence the network, or part of the network, must either contract to the full extent that the muscle-fibre does, or else be elastic and so follow the movements of contraction of the fibre.

Retzius<sup>2</sup> figures a specimen in which the longitudinal bars are zigzag. However, from his description, and from comparison with my own preparations, I believe this to be due to disturbance during the preparation and not to be a normal condition.

We have now to consider whether the network is actively contractile or merely a passively elastic structure; or whether one part of it is contractile and the other passive. That both network and sarcous substance are contractile is improbable; for if the function of the network and the sarcous substance is identical, there is no apparent reason for the presence of the network. Differentiation in structure always implies differentiation in function.

#### ACTION OF THE LONGITUDINAL BARS OF THE NETWORK.

We have seen that the longitudinal bars of the network diminish in length and apparently increase in thickness during contraction, and that they always remain straight in all

<sup>1</sup> 'Text-book of Physiology,' Dr. Michael Foster, 4th ed., p. 101.

<sup>2</sup> Loc. cit., plate i, fig. 19.

conditions of contraction and relaxation of the fibre. The question now before us is to determine if they are actively contractile or passively elastic. The following considerations are opposed to the latter view.

(a) If the longitudinal bars of the network are passively elastic they must be on the stretch in the relaxed condition of the fibre, and resemble stretched elastic threads running the whole length of the muscle-fibre. Now, when a muscle is cut out of the body, and thereby removed from its attachments, it does not contract to any considerable extent; therefore, supposing the longitudinal bars to be elastic, something must keep them on the stretch.

(i) This cannot be the sarcoous substance, for as it is semi-fluid in nature it can hardly keep elastic threads on the stretch.

(ii) It cannot be a nervous impulse, continually acting on the longitudinal bars, for if it were so a muscle would contract on section of its nerve.

(iii) The only force which can keep the bars on the stretch must be that of the transverse networks. On this supposition the uncontracted muscle is not in a state of rest, for there is a continual force exerted against the transverse networks by the tendency of the longitudinal bars to shorten. It is very difficult to conceive that the muscle, in its uncontracted condition, should be in a state of extreme tension, and not of comparative rest.

(b) In the unstriped muscle-fibre there are no transverse networks present, and hence no force to keep the longitudinal fibrils on the stretch, except the sarcolemma, which would be scarcely adequate to do so.

It therefore appears improbable that the longitudinal bars of the network are passively elastic, and if this is the case the only conclusion remaining is that they are actively contractile, and hence, presumably, the cause of contraction of the fibre. This view is also supported by the following considerations:

In the muscle-cell the part which performs the contraction is evidently the most fundamental part of the cell, and this we



should expect to be differentiated first. In the embryonic development of striped muscle it is found that the longitudinal striation appears first, i. e. that the longitudinal bars of the network are differentiated before the transverse. This is also the case in regenerating muscle. Again, in tracing the phylogeny of muscle, we found that the first indication of an intracellular network was in the vertebrate unstriped muscle in the form of longitudinal bars only. Hence both the phylogeny and the ontogeny of the network favours the view that the longitudinal bars are the contractile part of the cell.

#### ACTION OF THE TRANSVERSE NETWORKS.

Similarly to the longitudinal bars the transverse networks always remain straight in all conditions of contraction relaxation of the fibre. Hence they become necessarily extended when the muscle-fibre contracts, and return to their original form on relaxation of the fibre. The question now remains as to whether the return of the transverse networks to their original position is due to active contractility or to elastic rebound. The following arguments, for the first of which I am indebted to Mr. Melland, are in favour of the latter view.

(a) An elastic thread, if stretched and then allowed to rebound, will always return to its original length, i. e. will always shorten to the same extent. The transverse networks behave in this way; they always shorten to the same extent, viz. to the normal diameter of the fibre. This speaks in favour of their being passively elastic, for if they were actively contractile there is no reason why the fibre should not be compressed to less than its normal diameter, elongation at the same time taking place; whereas the fibre always relaxes to the same extent.

(b) If the statements of Gerlach, Retzius, and Bremer are correct, both parts of the network are connected with the end-plate and with the axis cylinder of the nerve, the longitudinal bars being connected indirectly through the transverse net-

works, the latter being in direct connection with the nerve. It is therefore difficult to conceive that the transverse networks can contract actively after the longitudinal bars have begun to relax, for the nervous impulse will apparently reach the former first, and hence they must contract at the same time as or before the longitudinal bars; and yet if the relaxation of the fibre is held to be due to active contraction of the transverse networks this is what must occur.

### CONCLUSION.

The conclusion to which I am therefore led is that the contraction of the striped muscle-fibre is due to the active contraction of the longitudinal bars of the network, and that the transverse networks are probably passively elastic, and by their rebound cause relaxation of the muscle-fibre. That the transverse networks and the muscle-corpuscles, with which they are said to be continuous, possibly furnish paths by which the nervous impulse is conveyed from the nerve ending to the longitudinal bars. That the contraction of the unstriped muscle-fibre is due to the active contraction of its longitudinal fibrils when these are present (as in vertebrate muscle). In the case of unstriped muscle which possesses no fibrils the contraction is due to the whole protoplasm of the cell, there being no special part differentiated to perform this function.

Should these conclusions prove to be correct, we may imagine the changes that occur in the striped muscle-fibre during contraction to be as follows:

The nervous impulse reaching the end-plate of the nerve is conducted by the transverse networks to the longitudinal bars, and causes them to shorten; it does not cause the transverse networks to contract, because they are passively elastic and non-contractile. The longitudinal bars shorten according to the strength of the nervous impulse, and remain so as long as it lasts. By fluid pressure the transverse networks are extended and remain so as long as the longitudinal bars remain contracted; when these cease to contract the elasticity of the

transverse networks comes into play, and they shorten to their original dimensions, and by fluid pressure extend the longitudinal fibrils to their original length, the elastic sarcolemma aiding in the process.

The alternate action of the longitudinal and transverse networks no doubt causes the special features of the contraction of striped muscle, viz. the quick response to stimulus and the rapid contraction; and we have seen that the network is developed wherever rapid movements have to be performed.

In connection with the foregoing considerations, the results of Gerlach, Retzius, and Bremer, should they prove to be correct, are of importance. I think there is little doubt that the longitudinal striæ described by Gerlach are identical with the longitudinal bars of the network figured by Retzius, Bremer, Melland, and myself. Gerlach traced these striæ into connection with the nerve endings. Retzius showed the connection between the muscle-corpuscle and the transverse striæ, and Bremer traced the axis cylinder of the nerve into direct continuity with the muscle-corpuscles. It therefore appears that the network is connected with the nerve, and that the longitudinal bars are connected with it indirectly through the transverse networks. The direct continuity of the network with the nerve does not necessarily imply that the network is itself nervous; in fact, it really supports the view that it is the part actively concerned in contraction; for we should expect a priori, that if a differentiation occurred in muscle it would be with the contractile part that the nerve would be in continuity.

On the other hand, with regard to the transverse networks, it is possible that they may be in part nervous in nature, and have for their function the more rapid conveyance of the stimulus through the muscle; and that the more rapid response to stimulus, the special characteristic of striped muscle, may be partly explained in this way.

There are two obvious objections to the theory of contraction we have arrived at, which I shall proceed to discuss:

1. It necessitates a difference between the longitudinal and

transverse bars of the same network. This is an objection, the real nature of which it is impossible to determine in the present state of our knowledge of the nature and import of intracellular networks in general. In unstriped muscle the longitudinal fibrils are alone present, and in the development of striped muscle the longitudinal elements of the network appear first. The transverse networks are described and figured by Retzius as direct processes of the muscle-corpuscles; the mode of their development is as yet unknown, but should they prove on further investigation to develop as processes of the corpuscles, it would follow that the two elements of the network are, in spite of their close connection in the adult, of entirely independent and different origin. And then a difference of function would become not only possible but highly probable. Further, the action of different reagents in splitting the fibre in different directions (alcohol, &c., causing longitudinal, and acids transverse splitting) lends some support to the same view. Haswell<sup>1</sup> in his observations on the striped muscle of the gizzard of *Syllis*, states that after treatment with hæmatoxylin, and then glacial acetic acid, the transverse networks are stained, but not the longitudinal; he says this may point to some difference in the substance of which they are composed.

2. This theory attributes the function of contraction to the network which forms much less of the bulk of the fibre than does the sarcous substance, the latter being far greater in amount than the network. In reference to this it should be borne in mind that contraction is not the only function performed by muscle. The muscles, as stated by Dr. Michael Foster,<sup>2</sup> are continually undergoing metabolism, giving rise to a certain amount of heat; the metabolism during rest being slow, but suddenly increasing during contraction. The energy involved in the work done in a muscular contraction is only about one tenth the total energy expended, the rest going out as heat. Hence the muscles must be regarded as the chief

<sup>1</sup> 'Quart. Journ. Micr. Sci.,' 1886.

<sup>2</sup> 'Text-book of Physiology,' 4th ed., p. 461.



sources of heat of the body, and are, "par excellence, the thermogenic tissues."

It thus appears that the thermogenic function of muscle absorbs a far greater amount of its energy than does the contractile function, and if we attribute the thermogenic function to the sarcous substance and the contractility to the network, the above objection appears to receive a satisfactory answer.

The following quotation from Prof. Michael Foster<sup>1</sup> is curiously in accordance with the view of the structure and function of muscle maintained above, and may fitly conclude this paper.

"It is quite open for us to imagine that in muscle, for instance, there is a framework of more stable material, giving to the muscular fibre its histological features, and undergoing a comparatively slight and slow metabolism, while the energy given out by muscle is supplied at the expense of more fluctuating molecules, which fill up, so to speak, the interstices of the more durable framework, and the metabolism of which alone is large and rapid."

#### SUMMARY.

1. In all muscles which have to perform rapid and frequent movements, a certain portion of the muscle is differentiated to perform the function of contraction, and this portion takes on the form of a very regular and highly modified intracellular network.

2. This network, by its regular arrangement, gives rise to certain optical effects which cause the peculiar appearances of striped muscle.

3. The contraction of the striped muscle-fibre is probably caused by the active contraction of the longitudinal fibrils of the intracellular network; the transverse networks appear to be passively elastic, and by their elastic rebound cause the muscle to rapidly resume its relaxed condition when the longi-

<sup>1</sup> Dr. Michael Foster, loc. cit., p. 475.

tudinal fibrils have ceased to contract; they are possibly also paths for the nervous impulse.

4. In some cases where muscle has been hitherto described as striped, but gives no appearance of the network or treatment with the gold and other methods, the apparent striation is due to optical effects caused by a corrugated outline in the fibre.

5. In muscles which do not perform rapid movements, but whose contraction is comparatively slow and peristaltic in nature, this peculiar network is not developed. In most if not all of the invertebrate unstriped muscle there does not appear to be an intracellular network present in any form, but in the vertebrate unstriped muscle a network is present in the form of longitudinal fibrils only; this possibly represents a form of network intermediate between the typical irregular intracellular network of other cells and the highly modified network of striped muscle.

6. The cardiac muscle-cells contain a network similar to that of ordinary striped muscle.

The investigations connected with this paper were partly carried on in the laboratories of the Owens College and partly at the Scottish Marine Station at Granton. I must here express my thanks to my brother, Professor Milnes Marshall, for his kindness in revising the paper, for much advice in its production, and for obtaining the literature of the subject; all the controversial points were discussed with him and the preparations submitted to his examination. My thanks are also due to Dr. Klein for kindly showing me his preparations and for examining several of my own. I must also thank Mr. J. T. Cunningham for the use of the Scottish Marine Station, and for obtaining several of the animals.

## DESCRIPTION OF PLATE VI,

Illustrating Mr. C. F. Marshall's paper on "Observations on the Structure and Distribution of Striped and Unstriped Muscle in the Animal Kingdom, and a Theory of Muscular Contraction."

[In all cases the gold chloride used was 1 per cent., the formic acid 25 per cent. The "usual gold method," when stated, means: 1 per cent. acetic acid for a few seconds, gold chloride thirty minutes, formic acid twenty-four hours in the dark.]

FIG. 1.—Ectoderm cell of Hydra: gold preparation. (1 per cent. acetic acid for a few seconds, gold chloride thirty minutes, formic acid one hour, exposed to sun.) *a*. Intracellular network. *b*. Muscular process. *c*. Intranuclear network.  $\frac{1}{10}$  immersion obj.

FIG. 2.—Portion of muscular fibre of Medusa. Usual gold method.  $\frac{1}{10}$  imm. obj.

FIG. 3.—Portion of muscle-cell of Earthworm, showing longitudinal rows of dots. Usual gold method.  $\frac{1}{10}$  imm. obj.

FIG. 4.—Muscle-fibre from adductor of Pecten, showing network. Usual gold method.  $\frac{1}{10}$  imm. obj.

FIG. 5.—Muscle-fibre from heart of Patella. (Acetic acid, 5 per cent., two minutes, gold thirty minutes, formic acid two hours, at 40° C.) Zeiss, J obj.

FIG. 6.—Crayfish heart, Gold preparation of. (Acetic acid, 5 per cent., a few seconds, gold twenty minutes, formic acid one hour, at 40° C.)  $\frac{1}{2}$  obj.

FIG. 7.—Muscle-fibre of Daphnia. (Acetic acid, 5 per cent., ten minutes, gold thirty minutes, formic acid two hours, at 40° C.)  $\frac{1}{10}$  imm. obj.

FIG. 8.—Muscle of Bird (left in formic acid three days).  $\frac{1}{10}$  imm. obj.

FIG. 9.—Muscle-cell from Rat's heart, showing network. Usual gold method. Zeiss, D obj.

FIG. 10.—Muscle-fibre from Frog's heart. (Osmic acid, 1 per cent., half an hour.)  $\frac{1}{10}$  imm. obj.

FIG. 11.—Network from heart muscle of Bird. (5 per cent. acetic acid fifteen minutes, gold thirty minutes, formic acid twenty-four hours.)  $\frac{1}{10}$  imm. obj.

FIG. 12.—Portion of unstriped muscle-cell from mesentery of newt, show-

ing intranuclear network and its connection with the fibrils of the cell. (5 per cent. amm. chromate twenty-four hours; logwood.)  $\frac{1}{10}$  imm. obj.

FIG. 13.—Part of fibre from bladder of Salamander, showing fibrils. Usual gold method.  $\frac{1}{10}$  imm. obj.

FIG. 14 *a*.—Muscle-fibre of *Dytiscus*, stimulated with alcohol vapour. Portion *a* relaxed. *b*. Contracted.  $\frac{1}{10}$  obj.

FIG. 14 *b*.—Network of relaxed portion.  $\frac{1}{10}$  imm. obj.

FIG. 14 *c*.—Network of contracted portion.  $\frac{1}{10}$  imm. obj.

FIG. 15.—Diagram of a muscle-fibre, showing change in network during contraction.

FIG. 16.—Diagram of the intracellular network of striped muscle. *a*. The transverse networks. *b*. The longitudinal bars of the network. (Copied from Melland, loc. cit., Diag. 1.)

FIG. 17.—Portion of network on a larger scale. (Copied from Melland, loc. cit., Diag. 2.)

FIG. 18.—Portion of muscle-fibre of *Dytiscus*, showing the network very plainly. One of the transverse networks is split off, and some of the longitudinal bars are shown broken off. (Copied from Melland, loc. cit., fig. 6.)

FIG. 19.—Hypothetical diagram of the termination of nerve in muscle-fibre and the connection with the network; based on views discussed in the paper. *S*. Sheath of Schwann, continuous with sarcolemma. *n*. Axis-cylinder branching and connected with muscle-corpuscles. *m*. Muscle-corpuscles connected with transverse networks.





**On the Fate of the Muscle-Plate, and the Development of the Spinal Nerves and Limb Plexuses in Birds and Mammals.**

By

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With Plates VII and VIII.

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THE late Professor Balfour<sup>1</sup> showed that the spinal nerves in Elasmobranchs spring entirely from epiblastic origins, and the same has been proved conclusively regarding the roots at least of the spinal nerves in birds and mammals, by the researches of Milnes Marshall,<sup>2</sup> His,<sup>3</sup> and others. The most complete account of the early stages in the development of the nerves in higher Vertebrates is that of Marshall.<sup>2</sup> He has traced the roots of the nerves from their origin from the spinal cord to the point when they unite together to form the mixed nerve. From that point onwards there is uncertainty. Though it is considered highly probable that the further growth of the nerves consists of an extension towards the periphery of the original epiblastic elements, still it has not been proved that this is so. It has not hitherto been shown that the nerve-trunks, after the junction of the two roots, are not formed from the cells of the mesoblast.

<sup>1</sup> 'Monograph on the Development of Elasmobranch Fishes,' London, 1878.

<sup>2</sup> 'Journal of Anatomy and Physiology,' vol. xi, p. 491.

<sup>3</sup> "Ueber d. Anfänge d. Peripherischen Nerven Systems," 'Archiv f. Anat. u. Phys.,' 1879.

The present investigation has been undertaken with the object of tracing the nerves in their development from the condition in which previous embryologists have left them, to a point at which they may be fairly compared with the adult state.

Chick embryos, artificially incubated, have been used for the most part. By means of series of continuous sections, cut in different directions, the nerves have been traced from end to end in the different stages of development, from their first appearance up to the formation of trunks having an arrangement closely similar to that found in the adult. These sections have been compared with sections of mammalian embryos of different ages, with the result that the condition of development of the nerves has been found to be identical in both at periods in which the development of other parts and organs of the body is the same.

The methods adopted were in almost all cases the same. For hardening the Mammalian embryos, Kleinenberg's solution of picric acid was used; for the Chick embryos, a cold saturated solution of corrosive sublimate. A solution of borax carmine was the staining agent employed, prepared according to Balfour's directions. The sections were cut with a Jung's microtome, fitted with an ordinary razor.

The earliest stages in the development of the spinal nerves in the Chick have been described by Marshall. He has shown that they spring from the spinal cord as buds, of which the dorsal are the first to appear, arising from the summit of the cord. The more anterior of the dorsal roots arise from a "neural ridge," an elevation continued back from the hind brain. By the interstitial growth of the dorsal portion of the spinal cord these roots become separated, and their attachments to the cord more laterally placed. The ventral roots appear at a later date. Projecting outwards directly, they unite at an acute angle with the dorsal roots to form the mixed nerve. The spinal ganglion on the dorsal root is evident before the fusion of the two roots occurs; it is formed by the proliferation of the cells of the bud which form the

root. The spinal nerves are thus formed in pairs, which occupy the intervals between the muscle-plates.

Before tracing the further growth of the nerves from this point, it is necessary to describe the destination of the muscle-plates and the mode of formation of the limbs, as in their onward development the nerves present differences according as they occur in relation to the limbs, or in the intervals between them.

### I. FATE OF THE MUSCLE-PLATE.

The dorsal and ventral roots of the nerves unite towards the end of the third day. But even before this time the limb buds have begun to appear (at sixty hours). The growth and differentiation of these buds, and the relations of the muscle-plates in the different regions of the body, complicate the process of nerve development.

In a Chick embryo, at the age of three days, when transverse sections are made through the trunk between the limbs, the muscle-plate (*m. p.*, fig. 1) is seen as an elongated column of cells lying directly beneath the epiblast, and separated from the spinal cord by the spinal ganglion (*sp. g.*) and roots of the nerve (*N.*). The lower end lies outside the angle (*a.*), between the somatopleure and splanchnopleure. The nerve-roots alternate with, and lie at a deeper level than, the muscle-plates. The muscle-plate itself consists of a double layer of cells, continuous at the ends, and separated from each other by a very evident line, the remains of the original cavity between the two strata. The outer layer, whose thickness is made up of several cells, consists of ovoid, spindle-shaped, or rounded cells, fitting closely together, and with their long axes directed from without inwards. They are sometimes multinucleated, and stain deeply with carmine. Round the ends of the muscle-plate they merge with the cells of the inner layer. The inner layer of cells has different characters. As seen in longitudinal sections, it is composed of spindle-shaped cells, which lie close together with their long axes directed from before backwards.



Several of these cells occur in one somite in a line from front to back. In other words, the fibres are shorter than the thickness of the somite. In transverse sections the fibres appear rounded with large nuclei, and are more separated from one another. The cells at the upper and lower ends of the muscle-plate stain most deeply.

The bud which gives rise to the fore limb has at this date attained considerable size. It projects almost directly outwards from the side of the trunk (fig. 2), growing partly from the mesoblast above the angle between somatopleure and splanchnopleure, and partly from the somatopleure itself. It consists of a mass of mesoblastic cells, densely packed together, especially at the surface and distal end. Towards the origin of the limb the cells become more scattered. This mass of mesoblast is covered by a layer of epiblast, which presents two thickenings where the cells are in most active growth, one forming a cap, covering the pointed outer end, the other forming a ring round the root of the limb, and appearing in transverse sections as thickenings above and below the root of the limb. The mesoblastic cells are entirely undifferentiated as yet; they are rounded, and stain deeply. Embryonic blood spaces are found here and there. The position of the muscle-plate is different from what has been described in the region between the limbs. By the growth of the limb bud it has become separated from the somato-splanchnopleuric angle (*a.*). Its lower end reaches to about the centre of the upper half of the base of the limb, that part which is continuous with the intermediate cell mass. Moreover, the plate does not lie external to the angle of the body cavity: otherwise it has the same relative position as in the dorsal region to the parts which constitute the trunk at this period. Histologically, also, it has very similar characters. The differences are seen in the centre of the plate. The inner stratum of longitudinally arranged spindle-cells is thicker. It stains badly, and the nuclei of the fibres are large and well defined. The outer layer is thinner in the centre, becoming thicker when traced towards the end of the plate. The cells of this layer stain

deeply. They are scattered in the centre, becoming more closely packed at each end.

In Chick embryos at three days six hours (fig. 3), in the dorsal region the muscle-plate (*m. p.*) has extended a short distance down the body wall in the somatopleure. The central portion of the plate is thicker, owing to an accumulation of the longitudinal fibres of the inner layer. The cells of the outer stratum are still more separated in the centre, and do not stain so deeply. The layer as a whole is thinner. The ends of the plate still present the primitive condition of the cells, which are angular, packed close together, and stained deeply. In the region of the fore limb at this date (fig. 4) the muscle-plate (*m. p.*) has the same characters; but its position is different. Its lower end reaches no farther than midway between the dorsal attachment of the limb to the trunk, and the somato-splanchnopleuric angle.

Twelve hours later (at three days eighteen hours) these changes are seen to be more pronounced. In the dorsal region (fig. 5), owing partly to the increase in vertical extent of the embryo, the muscle-plate (*m. p.*) has become elongated, and at the same time thinned out. There is no distinct trace of an outer layer to be found, except at the ends of the plate. Here the cells retain their primitive character, and stain deeply. The rest of the plate consists entirely of longitudinally arranged fusiform cells. The muscle-plate has a peculiar bend, passing almost vertically downwards towards the body cavity, and then suddenly sweeping outwards to enter the body wall. Its lower end has passed still farther down the somatopleure, lying close to the inner side. In the fore-limb at this date (fig. 6) the muscle-plate retains its original position. It does not extend outwards farther than the somato-splanchnopleuric angle. Its histological characters are the same as in the dorsal region. The limb bud itself has increased in size, and is now directed downwards. The cells which compose it are still undifferentiated.

In embryos at four days, in the regions of the trunk between the limbs (fig. 7), the muscle-plate (*m. p.*) has extended down

through a third of the length of the body wall, lying close to the outer side of the body cavity. Its relations and structure are the same as before. Each end is surmounted by a cap of cells, which retain their primitive characters; rounded, fusiform, or angular, they stain deeply, and are plainly separated off from the main part of the muscle-plate. These cells can be traced on to the outer surface of the muscle-plate, where they gradually become lost. The main part of the plate consists of elongated fusiform cells. In the region of the fore limbs (fig. 8) the mesoblastic tissue of the limb still presents the same characters. The cells stain deeply, are round, ovoid, and often multinucleated; but still undifferentiated. The foetal vessels are better marked. The muscle-plate (*m.p.*) occupies its primitive position, ending below at the root of the limb. It has the same structural characters as in the dorsal region; but the undifferentiated cells, which stain deeply, are best marked at the upper end of the plate.

In embryos at four days twelve hours, in the trunk between the limbs, the muscle-plate (fig. 11, *m.p.*) has passed half way down the body wall, lying close outside the cavity. It now consists almost entirely of elongated spindle-cells. In the regions of the limbs further changes are taking place, but in which the muscle-plate takes no part. It remains within the body cavity, and ends below at the same limit as before (fig. 12, *m.p.*). Structurally it is the same. In the limb buds themselves the first changes occur at this date, in the formative blastema, which result in the production of the muscular and osseous systems. The nerve plexuses, as we shall see below, have been produced; and the resulting trunks have passed into the limb, in two groups, one dorsal (*d.*) the other ventral (*v.*). Between, above, and below the nerves, the mesoblastic cells are taking on a characteristic arrangement. The cells immediately above and below each trunk (1, 2) are more closely packed together, forming thick layers, each several cells deep. They are histologically the same as before. In the centre of the limb bud (3), between the nerve trunks, the cells are now arranged in a concentric and symmetrical fashion, and are

separated from one another by a small amount of intercellular substance. Towards the dorsal and ventral surfaces of the limbs the cells are more scattered, so that the central portion of the limb in transverse sections appears darker than the superficial parts. At the free end of the limb (4) there is still no differentiation of tissue elements. The cells here form a simple mass, without any distinction into layers or groups.

In a five days' embryo the condition of the muscle-plate in the region between the limbs (fig. 13, *m. p.*) is much the same as at the last-mentioned period. It shows still further extension in a ventral direction down the body wall. In the same embryo, in the regions of the limbs the muscle-plate (fig. 14, *m. p.*) has clearly no connection with the muscular system of the limb itself. It consists now of elongated fibres, forming, in transverse sections, a column lying just outside the spinal cord and nerves, and separated from the surface of the body and from the limbs by a considerable thickness of ordinary blastema. The several tissues of the limb are formed from mesoblastic elements, developed in situ. A central core of cellular cartilage (3) is very evident at this date. The cells are arranged regularly in a concentric manner in transverse sections; in transverse rows in longitudinal sections. This cartilaginous cylinder is found in longitudinal sections to be broken up into segments, corresponding to the skeletal elements of the limb. The intercellular substance between the cells has largely increased in amount. At the periphery of this central mass the cells gradually become changed in character, being more deeply stained in mass, and individually becoming oatshaped or fusiform. The long axes of the cells are directed from within outwards. Two layers of cells thus appear, one above, the other below the cartilaginous bar. The cartilage, however, is not yet distinctly marked off, but is connected to these groups of cells by a definite and still more deeply-stained (perichondrial) layer. The nerves to the limbs derived from the plexuses have a very definite relation to these central groups of cells, which are enclosed within the nerve-trunks. The dorsal nerves pass over, and the ventral trunks



beneath, this central area. Above and below the nerves two other more distinct groups of ovoid cells (1 and 2) are now apparent, collected each into more or less separate subsidiary bundles, and easily distinguished from the surrounding undifferentiated mesoblast by their shape, and by the fact that, being closely packed together, they stain more deeply en masse. The four simple, unsegmented strata of ovoid cells—of which two are dorsal, and lie above and below the dorsal branches of the nerves; two ventral, and having a similar relation to the ventral trunks—are evidently the precursors of the muscular elements of the limbs. They are quite distinct from the muscle-plates, and are separated from them by a large quantity of undifferentiated mesoblast. The blood-vessels of the limb have now attained a large size, and are regular in their arrangement. One large artery (*art.*) passes down the centre of the limb on its ventral aspect, lying among the nerves, and accompanied by a vein (*V.*).

It is unnecessary to follow the muscle-plate further. It has been shown that while it grows into the body wall between the limbs, and forms the basis of the longitudinal muscles of the trunk; in the region of the limbs, it remains in its primitive position and has no share in the formation of the limb-muscles. It is merely concerned here in forming the longitudinal muscles of the back. In the limbs themselves the muscles are produced by the further differentiation of the four dorsal and ventral strata, which have been described as appearing from the mesoblast-cells, at first undifferentiated, and forming the original limb bud. In Chick embryos at six days, these strata of ovoid cells have become more fusiform, and are collected into more definite and separate systems. Two days later the muscles throughout the body are seen distinctly.

## II. DEVELOPMENT OF THE SPINAL NERVES AND LIMB PLEXUSES.

The later development of the spinal nerves naturally divides itself into two parts: firstly, in relation to the limbs; and secondly, in the trunk between the limbs. In essential points

the processes are the same in all regions of the body. The formation of the limbs, however, and the peculiarities in the position of the muscle-plates give rise to certain differentiations in the arrangement of the nerves in those regions.

In Chick embryos at three days (figs. 1 and 2), both in the trunk between the limbs and in the regions where the limbs are being formed, the nerves have reached the same stage of development. The nerve-roots, which lie within and alternate with the muscle-plate, have joined together. From their fusion a slender, finger-like process of cells results (*N.*), which represents the commencing nerve-trunk. The dorsal root is oval in transverse section, the ganglion, which is very large, forming nearly the whole of it. The nerves and their roots consist of large ovoid cells, containing often two or three nuclei, the long axes of the cells being directed outwards from the cord. They stain more deeply than the mesoblast cells in which they lie, and are surrounded by a slight amount of feebly-stained intercellular substance.

Six hours later (at three days six hours), the slender stalk (*N.*, figs. 3 and 4), retaining the same position within the muscle plate, has grown downwards and outwards as far as the somato splanchnopleuric angle (*a*). It has the same relative position in the trunk and in the regions of the limbs, passing between the muscle-plate and cardinal vein (*c.v.*). But, owing to the difference of growth of the muscle-plates in the two regions, it has reached its lower end in the regions of the limbs (fig. 4); while in the trunk, the muscle-plate, having by this time entered the body wall (fig. 3), extends farther than the nerve.

This description corresponds with the condition of development of the spinal nerves and muscle-plates in the Rabbit embryo of seven or eight days. Both histologically and morphologically the nerves have reached the same state of development.

In Chick embryos of three days eighteen hours there is not much difference in the relative amount of the growth of the nerves. The whole embryo has, however, increased in size. In the trunk (fig. 5) the nerves cannot yet be traced into the

body wall. In the region of the limbs (*N.*, fig. 6) they have passed out beyond the lower end of the muscle-plate and beyond the angle of the body cavity. The marked change, however, at this date is in the histological structure of the nerves. The spinal ganglia are well-formed ovoid masses, composed of large ovoid cells with two nuclei, the cells having a general arrangement in vertical rows. The cells forming the nerve-trunks have become elongated, fusiform, with fibrillar processes at each end. The body of the cell does not stain well; the nucleus, large, oval, and with several nucleoli, lies in the centre of the cell, and stains deeply; the distal ends of the nerves in the regions of the limbs present a ragged appearance, due to the protrusion and separation of these spindle-shaped cells into the mesoblastic tissue.

At four days the histological change is more marked. The cells forming the nerve-trunks have become more fibrous, the nuclei are less numerous, and the trunks stain yellow en masse. Both between the limbs and in relation to the limb buds the growth of the nerves has continued. In relation to the limbs (*N.*, fig. 8), the nerves sweep round between the lower ends of the muscle-plates and the body cavity, and, reaching the base of the limb, spread out, and then divide into a sheaf of branches, which diverge in the formative blastema of the limb. In the trunk between the limbs the nerves (*N.*, fig. 7) have extended a great way down the body wall, lying between the muscle-plate and the body cavity, but not reaching as far as the lower end of the plate. They divide, as in the limb, into branching processes, some of which pass directly outwards into the muscle-plate and divide again; some pass on, lying within the muscle-plate.

It is at this period that I have first been able to make out satisfactorily the existence of the trunk passing to join the sympathetic. A slender cord arises from the spinal nerve midway between the junction of the roots and the distal end. It courses inwards at right angles to the main trunk, and is soon lost. Now also the formation of the superior primary division of the nerve is first seen distinctly. It is constructed in the

same way in mammals, and is seen still more clearly in Rat embryos at fifteen to seventeen days (fig. 16). Each root of the nerves divides into two unequal branches—the dorsal root beyond the ganglion, the ventral root directly. Of these branches the smaller is superior, the larger inferior in both cases. The larger branches unite to form the main trunk of the nerve, or the inferior primary division; the smaller branches combine to form the superior primary division. This is directed upwards and outwards, and subdivides as it passes towards the surface.

In Chicks at four days six hours, the condition of the nerves in the trunk between the limbs is slightly more advanced, but presents no change of any note. In the regions of the limbs, however, the plexuses are now formed. In transverse sections through the embryo, the nerves are found, on entering the limbs, to divide into two fairly well-defined strands, separated by a central mass of mesoblast, which is in active growth, and preparing to form the cartilaginous basis of the limb. The nerves, in fact, spread out around this central core, and arrange themselves into two sets, one dorsal the other ventral. These dorsal and ventral branches of the nerves only pass a short distance into the limbs, and are not so well defined as in embryos a few hours older. But even now the process of plexus formation may be seen.

When longitudinal vertical (sagittal) sections are made continuously through the body, it is seen that the nerves to the limbs, besides forming the dorsal and ventral branches above mentioned, unite with adjacent nerves at the root of the limb to form a well-defined plexus. In the Fowl three main trunks form the brachial plexus,<sup>1</sup>—the first thoracic and the last two cervical nerves, with in addition a small branch from the more anterior cervical nerve. When sagittal sections are made, the limbs being divided transversely at their roots (fig. 9, *a*), the axillary artery (*art.*) and vein (*v.*), with the three main nerves (*N.*, 1, 2, 3), are divided just outside the body cavity (*B. C.*), and as they lie in the body wall (*B. W.*), before their entrance

<sup>1</sup> Macartney, Art. "Birds," 'Rees's Cyclopædia.'



into the limb bud, and below the terminations of the muscle-plates. In successive sections, from within outwards, these nerves can be traced to their terminations in the limbs. They first spread out, and approach one another, as described; in doing so they unite with adjacent nerves, so that the next step in the proceedings (fig. 9, *b*) is the formation of a plexiform mass of nerve-tissue (*plex.*), which encircles the artery. At the same time that this plexus formation occurs the division into dorsal and ventral branches is beginning. In the figure the axillary artery in the centre, with a group of mesoblast cells running up and down from it, shows the commencing separation of the mass into these two portions. In sections made a little farther outwards, the plexus gradually separates completely (fig. 9, *c*) into a dorsal and a ventral mass (*d.* and *v.*), each consisting of a broad, flattened band, separated by the artery and some mesoblastic cells. Still farther out, just before the limb is completely separated from the trunk (fig. 9, *d*), the nerves appear as two distinct cords (*d.* and *v.*). These gradually divide, become attenuated, and disappear as they are traced towards the distal portion of the limb. Exactly the same process occurs in relation to the nerves of the hind limb. When oblique longitudinal sections are made at this date, so as to cut through the length of the nerves (fig. 10), they are seen to spread out and divide laterally, so as to unite with similar branches (dorsal or ventral) of adjacent nerves, to form the plexus at the root of the limb. As already stated, there is no trace whatever at this date of either cartilage or muscle in the limb, which consists entirely of undifferentiated blastema.

In embryos, four days twelve hours old, the nerves have reached a more advanced stage of development. In the trunk between the limbs (fig. 11, *N.*) the nerve, which twelve hours earlier divided into a sheaf of branches in the body wall, now splits into two well-defined and unequal branches at a point just beyond the somato-splanchnopleuric angle. The larger branch continues the direction of the main nerve, and can be traced for some little distance between the muscle-plate and

body cavity. The smaller nerve represents the lateral branch of the adult, and is directed downwards and outwards through the muscle-plate, on the outer side of which it divides and is finally lost. The cord to the sympathetic nerve can be followed farther than before; but I have been unable to trace its connections with the roots and trunk of the spinal nerves.

In the limbs the early changes occurring in the blastema, which lead to the production of the osseous and muscular systems, have already been described. The nerves are of large size, and can be traced more than halfway through the limb towards the distal end. At the root of the limb the main trunk (fig. 12, *N.*) can be seen in transverse sections to divide into two well-defined trunks, which are clearly homologous with the terminal branches of the nerve in the region of the trunk at this date (fig. 11). These two large nerves are respectively dorsal (*d*) and ventral (*v*); and enclose between them the densest portion of the blastema (3). This enclosed portion has already been described as consisting of three parts—a central part, which is going to form cartilage, and a dorsal and ventral part, the elements of muscular tissue. On the dorsal surface of the dorsal nerve, and on the ventral surface of the ventral nerve, are other layers of mesoblast cells (1 and 2) undergoing division preparatory to the production of muscles. In longitudinal sections the three main nerves supplying the fore limb can be traced as before in successive sections, each dividing into dorsal and ventral branches; and these again uniting with adjacent nerves to form two flattened bands, which pass to the dorsal and ventral surfaces of the limb.

The nerve-trunks are almost entirely fibrous now, with rows of deeply-stained nuclei arranged alone and among the wavy fibres. These are evidently the connective-tissue elements of the nerve-trunks. Towards their terminations the fibres are fewer and the fusiform nerve-cells more abundant.

In Rat embryos, between twelve and fourteen days old, exactly the same condition of development of the nerves is found as in the Chick at four days twelve hours. The state of development of the body generally is the same, the limbs exist

as buds projecting downwards and outwards from the trunk, and composed, for the most part, of undifferentiated blastema. In the centre of this the cells are more closely massed together than at the periphery, and are being arranged concentrically to form the cartilaginous basis of the limb. Each of the roots of the nerve divides into upper and lower branches, which respectively unite; the upper branches to form the superior primary division, the lower to form the inferior primary division of the nerve. The latter is the main trunk. Passing downwards and outwards below the muscle-plates, it reaches the base of the limb where it divides into two branches, one dorsal the other ventral, with regard to the cartilaginous core. These branches can be followed through the limb, actually as far as the epiblastic surfaces and almost to the distal end. In minute structure the trunks very much resemble the nerves in the Chick, the chief difference being that the fusiform cell elements are more evident throughout.

In Chick embryos, at five days, the changes in the nerves between the limbs are not marked (fig. 13, *N.*). The lateral and inferior branches are well defined, and the whole nerve has passed farther down the body wall. From this time onwards these trunk nerves present no marked differences in morphological arrangement from what is found in the adult.

In the regions of the limbs at this date, as already described, the cartilaginous basis and muscular elements have begun to make their appearance. The nerves themselves occupy a position with regard to these elements which is highly characteristic. The dorsal and ventral trunks (fig. 14, *d.* and *v.*) are each covered above and below by masses of specialised, oat-shaped cells, which represent the layers of dorsal and ventral muscles. These double dorsal and ventral muscular layers are also separated by the cartilaginous framework of the limb. The nerves themselves stain yellow; consist of extremely wavy fibres, and present no distinct nuclei. Deeply-stained connective-tissue corpuscles lie among the fibres.

At five days twelve hours the process of muscle and cartilage formation in the limbs is more advanced. The appearance of

the nerves in transverse section is much the same as before. In successive longitudinal (sagittal) sections (fig. 15) the nerves can be seen at the root of the fore limb, undergoing division and union in the brachial plexus in the same way as, but more definitely than in younger embryos (four days six hours, fig. 9). The three main trunks are seen first (fig. 15, *a*, *N.*, 1, 2, 3) in company with the axillary artery and vein. They then divide, in successive sections (figs. 15, *b*—15, *e*), into dorsal (*d.*) and ventral (*v.*) branches. The dorsal branches unite with dorsal branches, the ventral branches with ventral branches, to form the nerves of distribution to the limbs. The plexus-formation is now complete, and from this time onwards there is no change in the essentials of its formation, which tally with the condition of the adult brachial plexus. It is to be borne in mind that, though the plexus is completely formed, yet the muscular elements are in a simple condition. Muscles are not formed in anything approaching the complexity of the adult limbs sooner than the ninth day.

### III. CONCLUSIONS.

1. On the fate of the muscle-plate and development of the muscles of the limbs.

In Elasmobranchs the muscles of the limbs are formed by the muscle-plates which grow down, and as they pass the roots of the limbs give off small buds, which become separated off and form the starting point of the muscle formation in the limbs.<sup>1</sup> In higher Vertebrates, while it has been held probable<sup>2</sup> that the muscle-plates do not enter into the formation of these muscles, it has not been shown satisfactorily how they do arise and what becomes of the muscle-plates. It is evident from the foregoing details that the muscle-plates, in the regions of the limbs, stop short in their downward growth, do not pass farther than the base of the limb, and are not concerned in any way

<sup>1</sup> Balfour, 'A Monograph on the Development of Elasmobranch Fishes,' London, 1878.

<sup>2</sup> Kölliker, 'Entwicklungsgeschichte d. Menschen u. der höheren Thiere,' Leipzig, 1879.



with the production of the limb muscles. These are formed by the differentiation of the mesoblastic cells forming the primitive limb buds. These cells form, in the first place, a central cartilaginous bar, above and below which, in the second place, are developed a double dorsal and a double ventral layer of simple muscle, which later on becomes more complex in its arrangement and forms the muscles of the adult.

In the region of the trunk, between the limbs, a different disposition of the muscle-plates occurs. They grow down in the body wall and eventually become converted into the longitudinal muscles of the trunk. They do not, however, appear to assist in the formation of the sub-vertebral (hyposkeletal) muscles.

In both regions the growth and differentiation of the parts of the muscle-plates are alike. The outer layer disappears gradually; the inner layer of the plate being converted into the longitudinal fibres. The disappearance of the outer layer is possibly due to the conversion of the cells into longitudinal fibres, which merge with those of the inner layer; but this is not certain. In Elasmobranchs each fusiform cell extends from end to end of the muscle-plate.<sup>1</sup> In birds and mammals this is not so. Each fibre is considerably shorter than the breadth of the somite.

The chief point of interest here is in connection with the development of the limb muscles. They first appear as double layers of dorsal and ventral cells, which layers are simple, without segmentation, and derived from the mesoblast cells of the primitive limb bud. In Elasmobranchs<sup>2</sup> this stage in the development of the limb muscles is a secondary one, and is preceded by events which are omitted in higher Vertebrates. The process of evolution of the limbs in birds and mammals is therefore shortened. In Elasmobranchs a downward growth and a cutting off of part of certain muscle-plates occurs; the portions cut off undergo further growth, passing into the limb bud, fusing together, and becoming differentiated into dorsal

<sup>1</sup> Balfour, 'Comparative Embryology,' p. 552.

<sup>2</sup> Balfour, 'Monograph on Elasmobranchs.'

and ventral strata. In birds and mammals the same end is reached without these preliminary steps, and without the intervention of the muscle-plates. The definite relations which these simple muscular layers bear to the nerves of the limbs, throw light on the evolution of the limb plexuses. Each nerve, passing into a particular region of the limb bud, divides into dorsal and ventral branches, to supply the dorsal and ventral surfaces respectively of that particular portion. As the mesoblast forming the limb-bud becomes more differentiated so as to give rise to the muscular layers, the portions opposite to, and originally derived from, the same somites as the nerves become fused, forming simple muscular layers in the first place. The nerves therefore fuse together; the dorsal branches forming a dorsal band, and the ventral branches a ventral band, which pass out, and are finally lost in these simple muscular layers.

2. On the growth and development of the spinal nerves.

It is difficult to demonstrate clearly, but it is next to impossible to deny, that the spinal nerves are developed from epiblast throughout their whole length. From the numerous sections which I have examined at different periods of growth, I have traced the spinal nerves, not only the nerve-roots, but also the trunks and the plexuses, as a centrifugal growth from the spinal cord. The growth of the nerves is both interstitial and terminal. Consisting at first merely of rounded cells, in an active state of proliferation; in older embryos these become first ovoid and then fusiform, at the same time being less deeply stained with borax carmine. These fusiform cells, by the alteration of their protoplasm, become converted into nerve-fibres. Moreover, while this interstitial growth goes on, the trunk of the nerve is elongated by means of proliferation of the cells at the periphery, which retain a primitive character longer than those in the more proximal portion of the trunk. For example, when the cells are fusiform in the nerve near the cord, they are oatshaped at the distal end; when they are fusiform at the distal end of the nerve, they are fibrous in the proximal part of the trunk.

### 3. On the homologies of the spinal nerves.

Their development shows that the nerves which form the limb plexuses are homologous with the whole nerves in the regions between the limbs, where their arrangement is simplest, and not merely with the lateral branch, as Goodsir supposed.<sup>1</sup> The nerves in both regions first spread out into a ragged bundle. These bundles at a later period arrange themselves into two well-defined cords, the division from the main trunk having the same relative position in both. In the regions between the limbs these trunks represent the lateral and inferior branches; in the regions of the limbs they are dorsal and ventral in position.

### 4. On the development of the limb plexuses.

I have elsewhere shown<sup>2</sup> that in mammals, and as far as I have been able to make out, the same holds good for birds also, the limb plexus are formed on a definite plan, which is essentially the same in all the animals examined, and in relation to both fore and hind limbs. The nerves which form the plexus divide, in the first place, into dorsal and ventral branches. These divisions subdivide, and the secondary cords, whether dorsal or ventral, combine with the cords formed by the division of adjacent (dorsal or ventral) trunks to form the nerves of distribution. Any given nerve to the limb may be derived from any number of the spinal nerves constituting the plexus, but it is always formed by a combination of either dorsal or ventral nerves.

This mode of arrangement of the nerves in the plexuses is to be explained by a reference to their embryology, and the mode of development of the different parts of the limbs. The plexus formation is complete, and the nerves of distribution are formed in the embryonic limb long before the appearance of muscles. In the development of the nerves in the limbs the

<sup>1</sup> 'Edinburgh New Philosophical Journal,' New Series, vol. v, Jan., 1857; 'Anatomical Memoirs,' vol. 2, p. 201, 1868.

<sup>2</sup> Graduation Thesis, Univ. Edin., 1886, 'On the Spinal Nervous System in Mammalia,' "The Limb Plexuses of Mammals," 'Journal of Anatomy and Physiology,' vol. xxi, 1887, p. 611.

following steps occur. The primitive nerve, in the first place, grows out beyond the lower end of the muscle-plate, and reaches the root of the limb. It there, secondly, spreads out into an irregular series of processes, which pass into the undifferentiated tissue of the limb. Thirdly, these branches at a later date arrange themselves in two trunks, one dorsal, the other ventral, which extend still farther into the limb and enclose between them a mass of blastema, from which the cartilaginous basis of the limb is formed. Fourthly, the dorsal and ventral trunks fuse with adjacent dorsal and ventral trunks to form two broad flat bands, from which, still later, the individual nerves as found in the adult are produced.

The development of the muscular system of the limb, occurring after the formation of the nerves, corresponds with it exactly. The muscles appear first as simple double dorsal and ventral layers, among which the nerves pass as dorsal and ventral bands, formed by the fusion of adjacent dorsal or ventral divisions of the nerves of origin. As these muscular strata lose their simplicity and take on the complex arrangement of the adult, the nerves at the same time become more and more subdivided, until in the adult the primitive characters of both are considerably masked.

Still, in the adult mammal, it is evident that the more pre-axial nerves in the series supply the more preaxial portions, the postaxial nerves the postaxial portions of the limb,<sup>1</sup> and the combinations of dorsal divisions and ventral divisions of the nerves are distributed to those muscular and cutaneous areas which are derived respectively from the primitive dorsal and ventral surfaces of the embryonic limb bud.<sup>2</sup>

In conclusion, I wish to express my deep indebtedness to Professor Milnes Marshall, of Manchester, for much advice and encouragement during the prosecution of the above researches, and for his kind assistance in the preparation of the present memoir.

<sup>1</sup> Herringham, "On the Human Brachial Plexus," 'Proc. Roy. Soc.,' Jan., 1887.

<sup>2</sup> 'Journal of Anatomy and Physiology,' vol. xxi, July, 1887.



## EXPLANATION OF PLATES VII &amp; VIII,

Illustrating Dr. Paterson's paper "On the Fate of the Muscle-Plate, and the Development of the Spinal Nerves and Limb Plexuses in Birds and Mammals."

FIG. 1.—Semi-diagrammatic view of transverse section through the trunk of a Chick embryo at the end of the third day. Both spinal nerve (*N.*), with its roots and ganglion (*Sp. g.*) and muscle-plate (*m. p.*) are shown. The spinal cord, notochord (*No.*), aorta (*Ao.*), and cardinal vein (*C. V.*), are also indicated. The muscle-plate is just entering the body wall. The section is taken between the limbs.

FIG. 2.—View showing same structures in an embryo of three days in the region of the fore limb.

FIG. 3.—From an embryo of three days six hours old, showing the growth of the muscle-plate (*m. p.*) and spinal nerve (*N.*) in the trunk between the limbs.

FIG. 4.—From the same embryo in the region of the fore limb.

FIG. 5.—From an embryo aged three days fifteen hours, showing the further growth of the muscle-plate (*m. p.*) and nerve (*N.*) in the trunk between the limbs.

FIG. 6.—Shows the same structures in the region of the fore limb.

FIG. 7.—From an embryo aged four days, with the muscle-plate presenting growing points at the two ends, and the nerve dividing in the body wall into a ragged bundle. The formation of the superior primary division (*s.*) of the nerve and the cord to join the sympathetic (*sy.*) are also seen.

FIG. 8.—From the same embryo, through the fore limb, showing the relative position of the muscle-plate and nerve. The nerve is seen dividing in the limb into a sheaf of branches.

FIG 9, *a.*—Longitudinal section through the body of a Chick embryo aged four days six hours in the region of the fore limb, cutting through the body wall (*B. W.*) just below the level of the muscle-plate. The body cavity (*B. C.*) is seen, and in the body wall are the three nerves (*N.* 1, 2, 3), and the artery (*art.*) going to the limb. *b.*—This section is made farther out at the root of the limb bud, and shows the thickening of the body wall, with the formation of the plexus, around the artery (*art.*). The vein (*v.*) is also seen. The nerves in the plexus are here on the point of separating into two bundles. *c.*—From a section made still farther out in the limb. The nerves, after forming the plexus, have more completely separated into a dorsal and a ventral bundle (*d.* and *v.*), with the artery in the middle. *d.*—Here the limb bud is

more apparent; it is becoming separated from the body wall; and the dorsal and ventral bands of nerve are well defined in the blastema.

FIG. 10.—From a longitudinal section through the body of the same embryo, in the region of the hind limb (*H. L.*), to show the lateral division and union of the dorsal and ventral divisions of the nerves to form the plexus (*plex.*). The spinal cord (*Sp. C.*) and spinal ganglia (*Sp. g.*) are also shown.

FIG. 11.—Transverse section through trunk of Chick embryo aged four days twelve hours, between the limbs, to show the muscle-plate and the spinal nerve. The division of the latter into its two terminal branches (*l. i.*) is seen.

FIG. 12.—Transverse section through the same embryo in the region of the fore limb. The spinal nerve is seen dividing at the root of the limb into dorsal (*d.*) and ventral (*v.*) branches. These enclose and are surrounded by masses of formative blastema (1, 2, 3), the precursors of the muscles and skeleton of the limb. The muscle-plate (*m. p.*) occupies its original position.

FIG. 13.—Transverse section through the trunk (between the limbs) of an embryo aged five days, to show the relative position and growth of the muscle-plate (*m. p.*) and nerve (*N.*).

FIG. 14.—Transverse section through the trunk and root of the fore limb of an embryo of the same age. *m. p.* Muscle-plate. *N.* Spinal nerve. *d.* and *v.* Dorsal and ventral divisions. 3. Commencing formation of cartilage in centre of limb, with a layer of dense blastema surrounding it. 2 and 1. Commencing formation of muscles above and below the nerve-trunks. *art.* Axillary artery. *v.* Axillary vein.

FIG. 15.—Successive longitudinal sections through the root of the fore limb of a Chick embryo aged five days twelve hours. The defined borders represent the body cavity. From *a* to *e* the nerves (*N.* 1, 2, 3) are seen to divide into dorsal and ventral branches (*d. v.*), which unite laterally to produce secondary dorsal and ventral trunks. *Art.* and *v.* Axillary artery and vein.

FIG. 16.—Diagram to illustrate the formation of the superior (*S.*) and inferior (*I.*) primary divisions of a spinal nerve from a Rat embryo. *Sp. C.* Spinal cord. *Sp. G.* Spinal ganglion. *No.* Notochord.  *Ao.* Aorta.



**Note on the Ciliated Pit of Ascidians and its  
Relation to the Nerve-ganglion and so-called  
Hypophysial Gland; and an Account of the  
Anatomy of *Cynthia rustica* (?).**

By

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With Plates IX and X.

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IN the adult Ascidians which I have examined, I find four main variations of the ciliated pit.

(1) In *Clavellina* the ciliated pit (fig. 1, *C.P.*) is simple in shape, its opening into the mouth being round in section. It lies ventral to the nerve-ganglion (*N.G.*), into the solid substance of which it leads by a wide opening (*B.*), situated near the anterior end of the ganglion. Behind the opening it narrows, and passes on into a canal (*C.*), lying immediately ventral to the ganglion. The cells lining this canal are flatter than those at its orifice, and are not ciliated. A large number of glandular tubes (*Gl.*) lie ventral to it and open into it. Seeliger<sup>1</sup> states that the hypophysial gland never attains to the complicated condition, which Julien<sup>2</sup> describes in some simple Ascidians. I find, however, that the gland is large and made up of branching tubes which open into the backward

<sup>1</sup> Seeliger, O, "Die Entwicklungsgeschichte de socialen Ascidien," 'Jenaische Zeitschrift für Naturgewissenschaft,' 1885.

<sup>2</sup> Julien, Charles, "Recherches sur l'organisation des Ascidies simples, sur l'hypophyse et quelques organs qui s'y rattachent," 'Archives de Biologie,' Tome ii, 1881.



prolongation (*C.*) of the ciliated pit in a way precisely similar to that described by Julin.

(2) In *Amaræcium proliferum* the ciliated pit (fig. 2, *C.P.*) is shorter and simpler than in *Clavellina*. It consists of a funnel, communicating by a circular opening with the mouth, and is lined throughout by ciliated columnar cells. It lies immediately ventral to the ganglion, with which it has no communication. At its apex it opens (*P.*) into a mass of spongy tissue (*Ti.*) lying ventral to it, which has a definite boundary, but is not glandular in structure, appearing rather to consist of degenerated tissue, somewhat resembling the notochordal tissue of Vertebrate embryos.

(3) *Ascidia* and *Ciona*.—I have examined several species belonging to these genera, and have found that the condition is similar to that described by Julin<sup>1</sup> in several species of *Corella*, *Phallusia*, and *Ascidia*. The pit consists of a ciliated funnel passing into a canal. A mass of glandular tissue lies ventral to the canal and opens into it by a number of ducts. The opening into the mouth is sometimes circular, but more often horseshoe-shaped.

(4) The condition in *Phallusia mammillata* has also been described by Julin.<sup>2</sup> A large reservoir lies ventral to the ganglion, communicating with the mouth by a comparatively small orifice. A large number of small canals open into the reservoirs and also communicate with the atrial cavity by a number of secondary funnel-shaped openings. Round the funnels are situated masses of cells of a deep yellow colour.

#### CONDITION IN THE EMBRYO.

*Amaræcium* Embryo.—The embryo remains in the atrial cavity of the parent until it has attained to the fully-developed tadpole stage.

The nervous system then consists of four parts :

<sup>1</sup> Julin, *C.*, loc. cit.

<sup>2</sup> Julin, *C.*, loc. cit., "Deuxième Communication."

(1) An anterior dorsal part (fig. 3 (1)), exactly resembling in structure the ganglion of the adult.

(2) A mass (fig. 3 (2)) lying ventral and posterior to (1), composed of very large ganglion cells with very distinct nuclei and nerve-fibres.

(3) A nerve-cord (fig. 3 (3)) passing off from (2) into the tail.

(4) A hollow sense-vesicle lying to one side of (2), and consisting of a vesicle with thin anterior and thick posterior walls. The unpaired eye is embedded in the wall at its antero-dorsal angle, and the otolith is situated on its floor and projects upwards into its cavity. This is the only part of the nervous system which is hollow at this time.

The ciliated pit opens into the buccal cavity and thence passes back, lying ventral to the anterior part of the nervous system, penetrates the junction between (1) and (2), and continues its course on the dorsal side of (2), ending blindly (*E.*) not far from the atrial pore (*A.P.*). At two points it opens into the solid nervous substance: first (*B.*), at about the middle point of the ventral surface of (1); secondly (*R.*), on the dorsal surface of (2).

Maurice and Schulgin<sup>1</sup> failed to find the ciliated pit in the embryo of *Amarœcium*, and state that there is no connection between the buccal cavity and the nervous system. This connection was quite clear in all my sections in which the stomodæum and nervous system were definitely established.

Kowalevsky<sup>2</sup> states that in *Phallusia mammillata* the mouth communicates with the hollow anterior end (viz. sense-vesicle) of the nervous system by a pore, which eventually gives rise to the ciliated pit. It is possible that he may have overlooked the existence of the ciliated pit in the embryo, as in optical sections, with which he worked almost entirely, it might appear as a simple pore.

<sup>1</sup> Th. Maurice and Schulgin, "Embryogénie de l'*Amarœcium Proliferum*," 'Annales des Sciences Naturelles,' 1884.

<sup>2</sup> Kowalevsky, A., "Weitere Studien über die Entwicklung der Einfachen Ascidien," 'Arch. für Mikr. Anat.,' 1871.

Seeliger<sup>1</sup> observed the pit in the embryo *Clavellina*, though he found no connection between it and the nervous system.

Salensky<sup>2</sup> describes the ciliated pit in the embryo of *Salpa democratica* as a short tube forming a communication between the pharynx and the anterior end of the nervous system, which is at first hollow, but afterwards becomes solid.

Kupffer<sup>3</sup> found no communication between the mouth and nervous system in the embryo of *Ascidia mentula*.

Van Beneden and Julin<sup>4</sup> describe the ciliated pit in the embryo of *Clavellina rosaceus*, and also state that on its ventral side it communicates with a mass of tissue lying ventral to it which gives rise to the gland. From their figures I believe this mass of tissue to be homologous with what I have described above as the posterior ventral part of the nervous system in *Amarœcium*. In the latter I assume that this structure is a part of the nervous system on account of its histological features, and also from the fact that it connects the dorsal part of the nervous system with the nerve-cord of the tail.

#### COMPARISON OF CONDITION IN EMBRYO AMARÆCIUM WITH THE VARIOUS TYPES IN ADULT ASCIDIANS.

I have not worked out the development from the oldest unhatched embryo into the adult form owing to lack of material, so that the views here put forward must be merely provisional.

There can be little doubt that the part of the embryonic nervous system, which is found persisting in the adult, is the

<sup>1</sup> Seeliger, O., loc. cit.

<sup>2</sup> Salensky, W., "Ueber die Embryonale Entwicklungsgeschichte der Salpen," 'Zeit. für wissen. Zool.,' 1876.

<sup>3</sup> Kupffer, C., "Die Entwicklung der Einfachen Ascidien," 'Arch. für Mik. Anat.,' 1872.

<sup>4</sup> Ed. van Beneden et Ch. Julin, "Le système nerveux central des Ascidies et ses rapports avec celui des larves urodèles," 'Arch. de Biologie,' tome v, 1884.

anterior dorsal part, this being rendered probable both by the histological resemblance of the two structures, and also by the fact that their position with regard to the ciliated pit is the same in both cases.

The adult condition most nearly resembling that of the embryo *Amaræcium* is found in *Clavellina*. Here the ciliated pit retains its connection with the nervous system, communicating with the ganglion in precisely the same way as it communicates with the anterior part of the nervous system in the embryo *Amaræcium*. In both cases it then becomes narrower, passes on and ends blindly—the difference being that in *Clavellina* it communicates on its ventral side with the gland, in the *Amaræcium* embryo with the posterior ventral portion of the nervous system. The relation of the ciliated pit to the gland in *Clavellina* is identical with that of the ciliated pit to the posterior ventral part of the nervous system in the *Amaræcium* embryo.

In the adult *Amaræcium* the position occupied in the embryo by the posterior part of the brain and in *Clavellina* by the gland is filled with a mass of degenerated tissue, and the communication between the ciliated pit and the nervous system has been lost. In *Ascidia* and *Ciona* the degenerated tissue is replaced by a mass of somewhat complicated glandular tissue lying under the ventral wall of the ciliated pit and communicating with it.

In *Phallusia mammillata* the condition is still more complicated, the gland communicating with the peribranchial cavity by a number of secondary funnels, its opening into the mouth being comparatively small.

#### SUGGESTIONS AS TO THE FUNCTIONS OF THE CILIATED PIT.

Judging from the fact that in the embryo *Amaræcium* the ciliated pit is connected exclusively with the brain, it seems probable that its original function was the aeration of the brain; this mode of aeration being similar to that found in *Nemertines*. It is doubtful whether it originally opened to



the exterior, and was subsequently involved in the stomodæum, or whether its opening into the mouth is primitive. In *Amaræcium*, at any rate, it is almost certainly epiblastic in origin, as it is derived from the epithelium of the stomodæum and not from the pharynx, as has been stated by Seeliger<sup>1</sup> for *Clavellina*.

Since, as mentioned above, it has in the late embryo no connection with any other structure than the brain, any other connection which exists in the adult is probably secondary.

In the adult no trace of the posterior part of the brain is found, but occupying its place in *Amaræcium* is a mass of degenerated tissue, which is connected with the exterior by means of the ciliated pit.

In *Ascidia* and *Ciona*, and apparently most other simple *Ascidians* (cf. *Julin*, loc. cit.), the function of the ciliated pit is to act as a duct for the so-called hypophysial gland (*Julin*) which lies in the position occupied in the *Amaræcium* embryo by the posterior part of the brain.

In *Clavellina* the ciliated pit has a twofold function.

(1) It communicates with the brain, and probably aerates it.

(2) Its posterior part acts as a reservoir to carry off the secretion of the gland.

There is thus a gradual transition from one function to another in the different types; the primitive condition, as an organ for the aeration of the brain, is found in the *Amaræcium* embryo, and is retained in *Clavellina*, while in the latter the secondary function, viz. that of an excretory duct, is also acquired.

In most adult forms (e.g. *Amaræcium*, *Ascidia*, and *Ciona*) the primitive function is lost, the secondary one only being retained.

The gland is possibly an altogether secondary structure, being developed to supply the need of an excretory organ in the anterior part of the body. It reaches its highest degree of complication in *Phallusia mammillata*.

<sup>1</sup> Seeliger, O., loc. cit.

If the excretory function of the ciliated pit be merely secondary no homology can exist between it and the proboscis pore of *Balanoglossus*,<sup>1</sup> or the external opening of the left anterior pouch from the fore-gut, described by Hatschek<sup>2</sup> in *Amphioxus*.

It is more probably homologous with the hypophysis of Vertebrates, the original functions of which may have been the aeration of the brain. When a complete blood-supply to the head was effected aeration by this means would no longer be required, and since a definite and complete excretory system had been at the same time developed, there would no longer be any necessity for an excretory organ in this position. Thus the hypophysis at the present time may represent merely a rudimentary condition of the gland and ciliated pit in Ascidians, having almost atrophied, and quite lost its function as a consequence of the development of the ordinary Vertebrate excretory system.

It is possible that the pineal gland of Vertebrates may represent the dorsal continuation of the ciliated pit in the embryo *Amarœcium* (fig. 3, *E*).

### THE ANATOMY OF CYNTHIA.

Whilst investigating the condition of the ciliated pit in various genera of Ascidians, I observed several features in *Cynthia*, which, as far as I know, have not hitherto been described. I have therefore thought it worth while to publish a short account of the general anatomy and histology of the species I have studied, which I believe to be *Cynthia rustica*.

N.B.—Some of the generic characters, in which the *Cynthiidae* differ from the *Molgulidae*, have been pointed out by

<sup>1</sup> Bateson, W., "The Later Stages in the Development of *Balanoglossus Kowalevskii*, &c.," this Journal, 1885.

<sup>2</sup> Hatschek, B., "Studien über Entwicklung des *Amphioxus*," 'Arbeiten aus dem Zool. Inst. Wien,' 1882.

Lacaze-Duthiers;<sup>1</sup> and Herdman<sup>2</sup> gives a short account of some forms found by the Challenger.

#### EXTERNAL CHARACTERS.

The individuals are small, varying in length from half to little more than an eighth of an inch, and each is almost as broad as it is long. It is wide and flattened at its base, by which it is attached to the rock, there being no stalk or peduncle. A great number of individuals live upon the same piece of rock, and are very closely applied to one another by their sides, so as to form a compact mass; but any one can be easily separated from the rest. The lateral pressure to which they are thus subjected causes the individuals to vary much in shape.

In colour they are a bright brownish red. They are quite opaque, so that it is not possible to make out any of the internal structure without removing the test.

The oral and atrial apertures are four-lobed.

#### THE TEST.

The test, which gives the red colour to the animal, is fairly thin, and in life is so closely applied to the body wall that it is difficult to remove it without tearing the epidermis. After preservation it can be removed with comparative ease, although it still adheres to the body wall. Except at its base, where fragments of the rock on which it lived generally remain attached to it, the test is free from sand, calcareous spicules, or other foreign matter.

As seen in sections it is composed of a homogeneous matrix with a few scattered cells. It also possesses a complicated system of vessels, which are lined by short columnar cells. In picrocarmine-glycerine preparations of the test these vessels are clearly seen, as well as numerous pigment cells, which are

<sup>1</sup> Lacaze-Duthiers, Henri de, "Histoire des Ascidies Simples des Côtes de France," 'Archives de Zool. Exp. et Gen.,' tome vi, 1877.

<sup>2</sup> Herdman, W. A., 'Challenger Report on the Tunicata,' Part I, "Ascidia simplices."

of two kinds, one appearing dark brown or black, and the other a bright orange.

### BODY WALL AND BODY CAVITY.

Beneath the test and closely applied to it is a layer of columnar cells (figs. 12 and 15, *Ep.*) with very definite nuclei. Their internal ends are rounded and they do not rest upon any basement membrane.

Beneath the epidermis is a thin layer of circular muscle-fibres (fig. 15, *c. m.*), then a thin layer of longitudinal fibres (fig. 15, *l. m.*). Within the latter is a very thin layer of circular fibres (fig. 15, *c. m.*), and then a thick layer of longitudinal and oblique fibres (fig. 15, *l. m.*), which are arranged in large irregular masses, not definitely marked off from one another, or from the surrounding tissue (fig. 15). All the muscles are unstriated.

A mass of connective tissue, constituting a meshwork of fibres, fills up the spaces between the muscles and extends inwards as far as the lining of the atrial cavity (figs. 12 and 15 *Ps.*). Nuclei are sometimes visible (fig. 15, *c. t. c.*) at the points of junction of the fibres; these apparently are the nuclei of the connective-tissue cells, the cell protoplasm being so drawn out and branching as not to be apparent round them.

Among the meshes of the connective tissue and lying freely in it are three kinds of cells:

1. Cells filled with black pigment (fig. 15, *p. c.*). A nucleus is present in each.

2. Large, coarsely granular cells (fig. 15, *g. c.*), in which I have not been able to discover nuclei.

3. Cells which stain faintly (fig. 15, *b. c.*), and have large, deeply-staining nuclei. The cell protoplasm is very finely granular.

Thin laminae of this connective tissue (fig. 12, *Ps.*<sub>2</sub>) pass across the atrial cavity into masses of similar tissue (fig. 12, *Ps.*<sub>1</sub>), which surround the alimentary canal, thus acting as mesenteries.

Large, irregularly-shaped processes of this connective tissue



(figs. 12 and 15, *Ps. p.*) project into the atrial cavity along its outer wall, being only separated from it by the epithelial lining of the atrial cavity (figs. 12 and 15, *A. Ep.*) which covers them. Figure 12 is a diagrammatic transverse section through *Cynthia*, and represents the relation of these processes to the atrial cavity. They appear very conspicuously when the atrial cavity is opened, especially in the fresh animal. They are then seen as very large, opaque, white bodies, which fill up a considerable portion of the cavity. I am not aware that any analogous structure has hitherto been described in any Ascidian.

The connective tissue extends from the body wall inwards to the atrial epithelium (fig. 12, *Ps.*), and also surrounds the alimentary canal. There is therefore no body cavity, its place being occupied by what appears to be a system of sinuses, the third kind of cell described above being the blood-corpuscles. For convenience of description I shall hereafter speak of the sinuses as the pseudocœle; but I do not wish to imply that it is necessarily homologous with the so-called pseudocœle of some Invertebrates. There are no definite blood-vessels, the heart opening out at both ends into the sinuses. Strands also pass across the atrial cavity to the pharynx, the spaces in the branchial bars being continuations of the sinuses, plentifully supplied with blood-corpuscles (figs. 5 and 7, *br. b.*).

It seems probable that the function of the processes projecting into the atrial cavity is to expose a greater surface of the sinus to the influence of the oxygen contained in it.

#### THE ATRIAL CAVITY.

The atrial cavity is very capacious, extending beyond the posterior end of the alimentary canal. For the greater part of its extent it is divided completely into two halves by a partition, which passes along from the outer wall of the atrial cavity to the walls of the pharynx. This partition starts just behind the buccal cavity, follows the line of the endostyle, and curves round the posterior end of the pharynx on to its dorsal surface, where it passes along the line of the dorsal lamina,

and stops just behind the atrial pore. The whole of the alimentary canal behind the pharynx is situated on the left side of the partition (fig. 12, *St.* and *Int.*). Thus the alimentary canal, embedded in its own portion of the "pseudocœle," is completely surrounded by the atrial cavity except at those points where strands pass off connecting its "pseudocœle" with the "pseudocœle" in the body wall outside the atrial cavity, and forming the mesenteries described above.

The atrial cavity is lined throughout by a layer of flattish cells, lying upon a basement membrane (figs. 12 and 15, *A. Ep.*). The cells are rounded at their free ends, and have large nuclei. This layer, of course, extends over the portions of the pseudocœle surrounding the alimentary canal, and over the mesenteries.

The atrial pore is placed not far from the mouth on a short papilla.

#### ALIMENTARY CANAL.

The mouth leads into the buccal cavity, which passes into the large pharynx (fig. 4, *Ph.*). The endostyle extends round the posterior end of the pharynx, ceasing at the point where the œsophagus is given off. The œsophagus (fig. 4, *Oes.*) is short, and soon opens into the large sack-like stomach (fig. 4, *St.*), which, on its external surface, is marked by deep longitudinal ridges. The stomach lies on the left side of the pharynx, its long axis being at right angles to that of the latter. It passes into the intestine (fig. 4, *Int.*), which almost at once bends upon itself and runs back across the pharynx, almost parallel with the stomach. On reaching the level of the dorsal side of the pharynx it turns forwards almost at a right angle, and runs straight to the anus (fig. 4, *A.*), which is situated at a short distance from the atrial pore, at the point where the partition dividing the atrial cavity ceases.

Shortly after leaving the stomach the intestine appears to be dilated for a short distance (fig. 4, *Int. L.*); this appearance is due to its being surrounded here by a layer of liver-cells.

The buccal cavity is lined just within the mouth by a

portion of the test which grows into it. This cellulose lining acquires a covering of thin epithelium, and forms a circle of short, blunt, unbranched tentacles. Further down, the cavity is lined by high ciliated columnar cells, which are thrown up into papillæ. At the junction of the buccal cavity with the pharynx there is a circle of cirri, which are unbranched, and in transverse action are four-lobed (fig. 10), one lobe being much larger than the other three. Two of the small lobes bear tufts of cilia.

Outside the epithelial lining of the buccal cavity there is a layer of connective tissue, and around this a thick layer of longitudinal and circular fibres.

The ciliated pit is simple, having the conditions found in *Ascidia* and *Ciona*. Its opening into the mouth is crescent-shaped, and it passes back thence, as a simple tube lined by high columnar ciliated cells, below the ganglion, at about the middle of which it opens out into the hypophysial gland, which lies immediately ventral to the ganglion. It has no communication with the latter.

The Pharynx.—The endostyle starts from the point where the buccal cavity joins the pharynx, and passes round its posterior end, ceasing where the œsophagus passes off (fig. 4, *End.*). It is very similar to the endostyle of other *Ascidians*, bearing a tuft of very long cilia at its base and shorter ones at the sides of the groove (fig. 9, *c. c.*). Between the masses of cells, which bear the cilia, are situated groups of much higher cells (fig. 9), while on each side, between the most external masses of ciliated cells and the ciliated epithelium of the pharynx, there is a row of cells which appear to secrete mucous (fig. 9, *m. c.*), as they appear when seen in transverse section to be throwing out irregular processes towards the cavity. At the anterior and posterior end of the endostyle its open edges are fused, so as to form a tube (fig. 8). This is an interesting point, as tending to confirm the theory of its homology with the thyroid body of the higher Vertebrata.

A thin lamina (the "dorsal lamina"), covered by low columnar ciliated cells (fig. 5, *D. L.*), projects from the median

dorsal line of the pharynx a long way into it; a rod of skeletal tissue (fig. 5, *sk. b.*) is present near its base, and extends throughout its whole length.

The gill-slits are very numerous. The bars between them are composed of connective tissue, which is a part of the pseudocœle, and contains a great number of blood-corpuscles (figs. 5 and 7, *br. b.*).

The skeletal system is somewhat complicated. The slits (fig. 7, *br. s.*) are elongated longitudinally, and arranged in transverse rows. The rows are separated from one another by thick skeletal rods, and divided into sets of five by similar rods (fig. 7, *sk. b.*), which meet the former at right angles. In addition to this main skeletal system, there is a system of finer rods (fig. 7, *s. sk. b.*) which accompany the larger ones, and are connected together by longitudinal rods passing between every two gill-slits, and a transverse rod lying across the centre of each row of slits. This secondary system of rods lies on the internal face of the pharynx.

The bars themselves in transverse section (fig. 5, *br. b.*) are seen to be covered on the surfaces turned towards the slits by columnar cells provided with cilia, and on their inner and outer walls by flat non-ciliated cells. Their internal cavity, as already stated, contains a blood sinus.

The Œsophagus (fig. 4, *Es.*) is very short and simple, being lined with short, columnar, ciliated cells.

The Stomach.—The walls of the stomach are thrown up into deep glands, which run in a longitudinal direction along its whole length.

The mouths of the glands are lined by high columnar ciliated cells (fig. 6, *c. c. s.*), very closely packed together, with a smallish nucleus placed at about the centre of each cell. The portion of the cells towards the lumen stains very deeply.

These cells are separated from those forming the deeper part of the gland by a slight constriction (fig. 6, *c.*).

The latter (fig. 6, *s. c. s.*) are somewhat higher than the former, and are not ciliated. The nuclei are placed quite near the bases of the cells. They appear to be secretory cells, as



their protoplasm is rich in granules, and at their free ends many of them are prolonged into blunt processes (fig. 6), which project into the lumen, and only stain very faintly. In most of the cells these processes are not visible, but since they otherwise resemble those that have them, the difference would seem to be due to their being in a different stage of secretory activity. In such cells the end abutting on the lumen stains more deeply than the rest of the cell, and the two regions are separated in preserved specimens by a row of very deeply-staining dots. Among the cells a few leucocytes are scattered (fig. 6, *l.*). The glands are separated from one another by a portion of the pseudocœle.

The intestine is lined throughout by rather short, ciliated columnar cells (figs. 11, *Ep. Int.*).

When the intestine is viewed as a whole it is seen to be enlarged for a short distance (fig. 4, *Int. L.*) soon after leaving the stomach. This appearance is due to its being surrounded by the so-called liver-cells. These are large and oval, are closely applied to the wall of the intestine, and form a compact mass round it. In the fresh state they are bright orange in colour. Each cell is pear-shaped with its thin end in contact with the epithelium of the intestine (fig. 11, *L.*), and is surrounded by a somewhat thick fibrous coat (*f. l.*), which is thickest at the broad end of the cell. In preserved specimens the cells are filled with a coarsely granular substance (fig. 11, *g. l.*), which is mostly aggregated at the narrow ends, and contains highly refractive concretions.

I could not find any connection of these cells, either with one another or with the intestine, but it seems possible that as they lie so closely applied to the wall of the intestine, their contents may pass into its lumen between the epithelial cells, the passages being so small as to have escaped my notice. I am unable to offer any suggestion as to their probable function.

#### THE HEART.

The heart is a long, thin-walled vessel, lying in a pericardium, which is considerably larger than itself.

It curves round the posterior end of the body, following the line of the partition between the two halves of the atrial cavity. For the greater part of its length it is situated in the pseudocœle external to the atrial cavity, but the anterior end of it lies in the partition, i. e. immediately ventral to the endostyle. It extends backwards nearly as far as the œsophagus.

At both ends it opens out into the pseudocœle, anteriorly by a long narrow slit in its dorsal wall, and posteriorly by a terminal pore, so that there is apparently no closed system of blood-vessels, but the circulation is carried on only through the blood-sinuses which surround all the organs and fill all the spaces usually occupied by the body cavity.

The pericardium is entirely closed.

The same condition of a heart situated in a closed pericardium, and itself opening at both ends, is said by Seeliger<sup>1</sup> to exist in *Clavellina*. The gradual shutting off of the heart from the body cavity in the development of the embryo, as he describes it, explains how the adult condition may have been brought about in the case of *Cynthia*.

#### THE GENERATIVE ORGANS.

The generative organs are unpaired, and lie near the posterior end of the body in the pseudocœle, outside the right half of the atrial cavity (fig. 12, *O.* and *ts.*).

They are arranged in two long masses on the outer and inner sides of a cavity (fig. 14, *G. D.*), which is lined by flat cells, and opens posteriorly into the atrial cavity. The mass on the outer side consists of testes (figs. 12 and 14, *ts.*), that on the inner of ova (figs. 12 and 14, *O.*).

The testes (fig. 13) are large oval sacs filled with spermatozoa (fig. 13, *sp.*); each sac is lined by a thin membrane, outside which are bundles of muscles (*M. ts.*), and, especially at its outer end, large collections of pigment-cells. At its inner end, i. e. towards the cavity, it is drawn out into a short duct (figs. 13a, 14, *D. ts.*) lined by low columnar cells, which terminates

<sup>1</sup> Seeliger, Oswald, "Die Entwicklungsgeschichte der Socialen Ascidien," 'Jenaische Zeitschrift für Naturgewissenschaft,' 1885.

close to the wall of the cavity, but does not appear to open into it. It is possible that when the spermatozoa become ripe they pass down the duct into the cavity by an opening, which is temporarily established into it, the communication being closed at other times.

The ovary (fig. 14, *O*) lies on the opposite side of the cavity. It has no limiting membrane, the ova lying freely in the pseudocœle. There is no oviduct, but the ova, when ripe, probably break through the wall into the cavity, which thus serves as the common generative duct, conveying both male and female products into the atrial cavity.

Each ovum is surrounded by a single layer of cells, which either are follicle cells or give rise to the test.

#### THE NERVOUS SYSTEM.

The nervous system has the form generally found in adult Ascidians. It consists of a large ganglion lying between the mouth and atrial pore, and is composed of fibres, which are surrounded by a peripheral layer of ganglion cells. Anteriorly it sends off two nerve-trunks, which pass, one on each side of the mouth; posteriorly it also sends off two trunks, which very soon divide again into several small branches, whose course I could not follow for any distance.

#### THE HYPOPHYSIAL GLAND.

The hypophysial gland is a compact mass of tissue, lying immediately ventral to the ganglion. It consists of a great number of fine glandular tubes, which towards the dorsal side of the gland unite, forming larger ducts, which open into the caual of the ciliated pit.

## EXPLANATION OF PLATES IX &amp; X,

Illustrating Lilian Sheldon's "Note on the Ciliated Pit of Ascidi-ans, and its Relation to the Nerve Ganglion and so-called Hypophysial Gland; and an Account of the Anatomy of *Cynthia rustica* (?)."

*List of Reference Letters.*

*A.* Anus. *A. Ep.* Epithelium lining atrial cavity. *At.* Atrial cavity. *At. P.* Atrial pore. *B.* Communication between ciliated pit and ganglion. *b. c.* Blood-corpuscles. *br. b.* Branchial bar. *br. s.* Branchial slit. *C.* Canal of ciliated pit. *C. P.* Ciliated pit. *c.* Constriction between the two kinds of cells lining glands of stomach. *c. c.* Ciliated cells of endostyle. *c. c. s.* Ciliated cells lining mouths of glands of stomach. *c. m.* Circular muscles. *c. t. c.* Connective-tissue corpuscles. *D. L.* Dorsal lamina. *D. ts.* Duct of testis. *E.* Blind end of ciliated pit. *End.* Endostyle. *Ep.* Epidermis. *Ep. Int.* Epithelium lining intestine. *Ep. ph.* Epithelium lining pharynx. *f. l.* Fibrous coat of liver-cells. *G. D.* Common generative duct. *Gl.* Hypophysial gland. *g. c.* Granular cells of pseudocœle. *g. l.* Granular contents of liver-cells. *H.* Heart. *Int.* Intestine. *Int. L.* Part of intestine surrounded by liver-cells. *L.* Liver-cells. *l.* Leucocytes. *l. m.* Longitudinal muscles. *m. c.* Mucous cells of endostyle. *M. ts.* Muscles surrounding testis. *N. G.* Nerve ganglion. *O.* Ova. *Œs.* Œsophagus. *P.* Communication of ciliated pit with mass of tissue in *Amarœcium*. *Pc.* Pericardium. *Ph.* Pharynx. *Ps.* Pseudocœle. *Ps. p.* Processes of pseudocœle. *p. c.* Pigment-cells. *R.* Communication of ciliated pit with (2). *sp.* Spermatozoa. *st.* Stomach. *Stm.* Stomodæum. *s. c. s.* Secreting cells of stomach. *sk. b.* Skeletal rod. *s. sk. b.* Secondary skeletal rod. *T.* Test. *Ti.* Mass of tissue lying ventral to ganglion in *Amarœcium*. *ts.* Testis. (1) Anterior dorsal part of nervous system of *Amarœcium*. (2) Posterior ventral part. (3) Nerve cord to tail.

All the figures, except Figs. 12 and 4, were drawn with Zeiss's camera lucida. The objective and ocular with which they are drawn are mentioned in the description of each figure.

FIG. 1.—Longitudinal section through the ciliated pit, ganglion, and gland of *Clavellina*, showing the communication of the ciliated pit with the ganglion and gland. (Oc. 2, obj. A.)

FIG. 2.—Longitudinal section through the ciliated pit, ganglion, and gland of an adult *Amarœcium*, showing the ciliated pit quite shut off from the ganglion but communicating with the mass of tissue lying ventral to it. (Oc. 2, obj. D.)



FIG. 3.—Longitudinal section through the ciliated pit and nervous system of a larval *Amarœcium* immediately before hatching. The ciliated pit communicates with the two portions of the nervous system. (Oc. 2, obj. D.)

FIG. 4.—Alimentary canal of *Cynthia rustica*, seen from the left side. Drawn from a dissection.

FIG. 5.—Transverse section through the dorsal lamina of *C. rustica* and three branchial bars and slits. (Oc. 2, obj. C C.)

FIG. 6.—Transverse section through one of the stomach glands of *C. rustica*, showing the two kinds of cells by which it is lined.

FIG. 7.—A portion of the wall of the pharynx of *C. rustica*, showing the arrangement of the branchial slits and skeletal system. Drawn from a picrocarmine-glycerine preparation. (Oc. 2, obj. B.)

FIG. 8.—Transverse section through the anterior end of the endostyle of *C. rustica*, where its edges have fused to form a tube. (Oc. 4, obj. B.)

FIG. 9.—Transverse section through the endostyle of *C. rustica* in its middle region. (Oc. 4, obj. B.)

FIG. 10.—Transverse section through one of the cirri in the buccal cavity of *C. rustica*, showing its four lobes, two of which are provided with cilia. (Oc. 2, obj. D.)

FIG. 11.—Transverse section through a small portion of the wall of the intestine of *C. rustica*, showing the adjacent liver-cells with their fibrous walls and granular contents with concretions. (Oc. 2, obj. E.)

FIG. 12.—Diagrammatic transverse section through a *C. rustica*, near its base, showing the various organs and their relations to one another.

FIG. 13.—Section through a testis of *C. rustica*, showing it filled with spermatozoa and surrounded by a delicate membrane, outside which are muscles and pigment-cells. At one end it is seen to be continued into a duct. (Oc. 2, obj. C C.)

FIG. 14.—Transverse section through the generative organs of *C. rustica*, showing the testes, with their ducts, and the ova lying respectively on the outer and inner side of the generative duct. (Oc. 2, obj. A, reduced half.)

FIG. 15.—Transverse section through a small portion of the body wall and pseudocœle, showing the muscle layers and connective-tissue meshwork, with the different kinds of cells in it. A process from the pseudocœle projecting into the atrial cavity is cut through. (Oc. 4, obj. C C.)

## The Tongue and Gustatory Organs of *Mephitis mephitica*.

By

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With Plate XI.

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It is now twenty years since Christian Lovén (26)<sup>1</sup> and Gustav Schwalbe (37) discovered and described, independently of each other, the peripheral end-organs of the nerves of taste in the tongue of Mammalia. Subsequent investigators have studied the distribution and minute anatomy of these organs in many animals, and in all essential points they confirm the results reached by Lovén and Schwalbe.

Before passing to the consideration of my own observations I will briefly review what is known regarding the position and structure of the taste organs of Vertebrates.

Bellini, nearly two hundred years ago, considered the papillæ of the tongue to be organs of taste.

In 1846, Waller (50) investigated the epithelium of the fungiform papillæ of the frog, and also studied the cilia and ciliary movement. In 1847, he (51) concluded, from the experiments of Longet, that the glosso-pharyngeus was the nerve of taste for the base of the tongue and the lingual for the tip and anterior third. He succeeded in tracing nerves into the base of the fungiform papillæ of the frog, and into the papillary elevations on the tongue of the toad. He believed the fungiform or "neurovascular" papillæ to be the chief

<sup>1</sup> These figures refer to the bibliography at the end of the paper.

organs of taste in the frog. The soft palate has also, he says, the power of taste. The conical papillæ he considered tactile organs. In 1849 he (54) redescribed these organs, and also speaks of the gustatory nerves terminating in the fungiform papillæ on the dorsum of the tongue, and of a gustatory area situated at the summit of each papilla.

In 1851 Leydig (23) described in the external skin of fresh-water fishes certain beaker- or flask-shaped bodies, which he was disposed to regard as organs of a tactile nature. In 1857, he showed (24) that the epithelium covering the end surfaces of the fungiform papillæ differs from the rest of the epithelium. Later investigators, with the exception of Fixen, have confirmed this.

In 1863, J. E. Schulze (34) redescribed the beaker-shaped bodies of fishes, and considered them organs of taste. He found them in greatest number where the fibres of the glossopharyngeal nerve are most thickly distributed, i. e. in the mucous membrane of the palate, upon the gums and tongue rudiment, on the inner side of the gill arches, and upon the lips. In structure he found them to agree, in most respects, with the organs of taste of the frog. The beakers he described as composed of two kinds of cells, viz. Sinneszellen and Stützzellen, or sensory and supporting cells; the former having a peripheral and central process. In 1867, he stated (35) that the peripheral extremity of the taste-cell bears a fine hair-like process as in mammals. In 1870, Schulze (36) described, in the papillæ of the mouth of a larval amphibian (*Pelobates fuscus*), bodies resembling in structure the beaker-shaped organs of fishes, which he considered taste organs.

In 1872, Todaro (44) described, in the papillæ covering the rudimentary tongue of *Trygon pastinaca*, a number of club-shaped bodies connected with the ultimate ramifications of the glossopharyngeus nerve, which he regarded as organs of taste and analogous to those of mammals. At the base of the gustatory organ the nerve loses its sheath, and the fibrillæ of the axis cylinder separate and join the central processes of the taste-cells.

Jourdan quite recently (18) has pointed out on the gills and in the buccal cavity of the marmoset, cup-shaped bodies composed of central and peripheral cells, which, in structure and situation, differ completely from the organs of touch, and which he regards as taste-bulbs.

In 1858, Billroth (4) described the peculiar epithelium of the taste papillæ of the frog, and believed that certain of its cells were continuous with nerve-fibres. The smaller papillæ he thought were unprovided with nerves.

Hoyer (16) differed from Billroth in supposing that the nerves terminate bluntly beneath the epithelium.

In 1861, Key (19) described in the frog two kinds of cells at the summit of the fungiform papilla,—epithelial cells and taste-cells. He speaks of the penetration of the axis cylinder alone into the papilla, and its division into fibres which enter the taste-cells at its summit. The “nerve-cushion” of Engelmann he considered an enormous enlargement of the neurilemma and called it the “nerve-shell.”

Hartmann (10) thought that the nerves ended in plexuses beneath the epithelial cells of the fungiform papillæ.

Beale (2), Engelmann (7), and Maddox (29) supported Key, believing in a structural continuity between the cells at the top of the papilla and the nerve-fibres in its axis. The former, however, did not consider the cells to be of epithelial origin.

In 1868, Engelmann (8) described, in the fungiform papilla of the frog, numerous dichotomous subdivisions of the nerve-fibres, which form a close network and spread out in the lower half of the “nerve-cushion” in nearly a horizontal direction. The upper part of the papilla consists of a solid disc composed of non-nucleated connective tissue, which he calls the “nerve-cushion,” and upon which rests the taste disc. The latter is composed of three distinct kinds of cells, viz. cup-shaped, cylinder, and forked. The two former he considered were epithelial cells only. The forked cells he regarded as the end-organs of the gustatory nerve, probably being directly continuous with pale nerve-fibres, which in their chemical reaction they resemble. Engelmann says that the nerve-fibres just



before entering the "nerve-cushion" lose their medullary substance and neurilemma.

In 1869, Beale (3) redescribed the epithelium of the papillæ of the frog, and reiterated his disbelief in the existence of structural continuity between nerve-fibres and epithelial cells. He figured fine nerve-fibres ramifying in the connective tissue of the simple papillæ, and connected with them oval-shaped masses of germinal matter or nuclei, formerly supposed to be connective tissue. He believed in a connection between the cells upon the summit of the fungiform papilla and the nerve-fibres in its axis, but did not consider the former epithelial in structure. He figured a nervous plexus containing nuclei at the top of the papilla, the fibres of which are derived from the nerves in its axis, and from which fine fibres may be traced into the special organ composed of "epithelial-like" cells. He found that the bundle of nerve-fibres distributed to a papilla always divides into two, which pursue opposite directions; this division taking place either at the base of the papilla or at some distance from it.

In 1869, Maddox (29) regarded the fungiform papillæ as the chief organs of taste in the frog, and described the nerves of taste as possessing terminal organs consisting of nerve matter.

In 1867, Szabadföldy (43) described the nerves of taste as terminating in mammals in pear-shaped bodies lying in the mucous membrane of the tongue. Two years later Letzerich (22) called attention to a peculiar way in which these nerves end in the papillæ of the cat, ox, and weazel. In neither case have the results reached by these observers been verified.

In 1867, Lovén (27) described the taste-bulbs (*Geschmacks-zwiebeln*) or taste-buds (*Geschmacksknospen*) of mammals. He studied them in the circumvallate papillæ of the cat, rabbit, pig, sheep, calf, dog, horse, and man, and found them to consist of central and peripheral cells. The outer or cover-cells, for support and protection; the inner or taste-cells, bearing a central and peripheral process, the former being continuous with a nerve-fibril, the latter terminating in a delicate hair-like extremity which projects a short distance beyond the opening

of the bulb. He says that in man and the calf the gustatory nerve-fibres lose their medullary sheath in the outer layer of the mucous membrane, the axis cylinder being prolonged into the bulb, where it divides into terminal branches which are distributed to the taste-cells. In the calf the peripheral process of the taste-cell carries no hair at its extremity. Lovén found taste-bulbs and cells on the upper surface of the fungiform papillæ of the calf, rat, and rabbit, the small ones containing a single specimen only. He also detected in the rat and rabbit a few taste-bulbs in the outer wall of the trench encircling the circumvallate papilla.

In 1867, Schwalbe (37) published the preliminary report of his investigation of the "Schmeckbechers" in the papillæ of the sheep, ox, horse, dog, cat, and rabbit. His detailed account (38) of the taste-goblets of these animals, including also those of the deer, pig, guinea-pig, hare, and man, appeared the following year. His description of their location and structure agrees essentially with that given by Lovén. He found taste-bulbs in man and the dog on the outer wall of the trench surrounding the circumvallate papilla, and in the fungiform papillæ and lateral organ of taste of the pig. He notes in man and the sheep two kinds of taste cells, namely, staff-cells (Stabzellen) and needle-cells (Stiffchenzellen). He found in the sheep at the apex of the bulb, after treatment with perosmic acid, a circle of fine short hairs or cilia, which appeared to spring from the end of the cover-cells. In the sheep also, at the base of the circumvallate papilla, is a richly-developed nervous plexus. He speaks of the small branches of the glosso-pharyngeus being provided with ganglia, especially where the nerve divides at the base of the papilla.

Engelmann (9) found bulbs in the fungiform papillæ of the mouse and cat, and described them in the lateral organs of taste (papillæ foliatæ) of the rabbit and hare. He says that usually the central process of the taste-cell divides, at a short distance from the nucleus, into two branches. He speaks of groups of ganglion-cells in the branches of the glosso-pharyngeus ramifying beneath the taste-ridges of rodents, and points

out the resemblance in physical characteristics and chemical reaction of nerve-fibrils with the central processes of the taste-cells.

In 1869, v. Wyss (56) described the taste-bulbs in the papilla foliata of the rabbit and hare, and called attention to the analogous organs of man. In 1870, (57) he studied them in the circumvallate and fungiform papillæ of many mammals, including the hedgehog and squirrel; but failed to find them in the fungiform papillæ of man.

Krause (20) observed taste-bulbs in the fungiform and foliate papillæ of man, and v. Ajtai (1) described them in the papilla foliata of man and other mammals.

Hönigsmied (12 and 13) has shown the distribution of the taste-bulbs in the circumvallate and foliate papillæ of various mammals, and, in some, has found them occurring on the summit of the papilla, though these were usually smaller than those on the sides. By means of chloride of gold, Hönigsmied traced the nerve-fibrils directly into the taste-cells in the fungiform papilla of the cat, the cover-cells not being stained, while the taste-cells were. Vintschgan and Hönigsmied (47 and 49) found in the rabbit that, after section of the glosso-pharyngeus nerve, the taste-bulbs degenerate, while the cover-cells become changed into epithelial cells in a few months. Ranvier (32) repeated this experiment, and has met with a similar result.

Sertoli (41) states that he has traced nerve-fibrils directly into the taste-bulbs in the papilla foliata of the horse. In the fungiform papillæ of the same animal he says that the nerves terminate in an intra-epithelial plexus of fine non-medullated nerve-fibrils.

Hoffmann (14) found taste-bulbs on the summit of the fungiform and circumvallate papillæ of man, and also in some papillæ of the soft palate and upper part of the uvula. He failed to find in the epiglottis what he considered genuine taste-bulbs.

In 1868, Verson (45 and 46) described in the second fourth of the posterior surface of the epiglottis of man, certain "bud-like structures," which resembled mammalian taste-bulbs.

Krause (21) observed them on the dorsal surface of the epiglottis of the sheep and rabbit. Schofield (33) has described them in the lower half of the posterior surface of the epiglottis of the dog and cat, arranged in horizontal and vertical rows. He says that with each "goblet" is associated the duct of a mucous gland. In 1873, v. Ebner (6) pointed out that the serous glands always occur in the parts of the tongue that contain taste organs, and their ducts open into the furrows lined by the taste-bulbs. Davis (5) studied the bulb-shaped organs in the epiglottis of the cat, dog, calf, pig, rabbit, and man, and found them on the upper and lower parts of the posterior surface of that organ. In the dog he found them on the inner side of the arytenoid cartilages, on the aryepiglottic folds, and in the epithelium of the true vocal cords. He regarded them as terminal organs of the glosso-pharyngeal nerve. Simanowsky (42) has also seen them on the true vocal cords of man and the dog. In the vocal cord of the dog and rabbit he figures the nerve-fibres as terminating in pencil-shaped extremities. Hönigschmied has observed bulbs on the epiglottis of the deer and calf.

Poulton (30) has described, in a highly interesting and suggestive manner, the taste-bulbs of *Perameles nasuta*. The circumvallate papillæ, he says, are highly developed in shape and structure, and in the abundance of nervous and glandular tissue which they possess; but the terminal organs he considers of a low type. Within the papillary body is a large ganglion, which divides into branches running towards the sides of the papilla containing taste-bulbs. The nerve-fibres are chiefly non-medullated, but possess a distinct sheath of Schwann. He found near the top of a single fungiform papilla two bulbs of a low order. Poulton (31) found in the posterior region of the tongue of *Ornithorhynchus paradoxus* two pairs of gustatory areas. The anterior pair lie below the surface in a furrow, the floor of which is invaginated upwards into a ridge, which carries the taste-bulbs. The ridges of the posterior pair reach the surface. In both regions the bulbs are situated on the sides and upper surface of the ridges, and the ducts of



serous glands open into the spaces around them. The centre of the ridge is nearly filled by non-medullated nerve-fibres, which radiate outwards to end in the bulbs. The bulbs are developed at the ends of long papillary processes. Nerve-fibres can be followed into the bulbs where they pass between the cells in various places. Poulton suggests "that the primitive type of bulb was papillary in position and subepithelial in structure, and has gradually given way to a bulb that was interpapillary and epithelial."

Among recent observers who have studied the taste organs of mammals, especially with regard to development, are Lustig (28) and Hermann (11). The former has described the development of the taste-bulbs of man and the rabbit, and the latter has investigated the papillæ, circumvallatæ, and foliatæ of the foetal and newborn rabbit. In the papilla circumvallata of the latter Hermann found taste-bulbs on the summit. Boulart and Pilliet (58) have, within a short time, examined the tongues of a number of mammals, with special reference to the presence or absence of the papillæ foliatæ.

Holl (15) has lately studied the taste organs of *Salamandra maculata*. Goblet-shaped sense organs, or end-bulbs have been described by Leydig (25) in the skin and mouth of various snakes, and Wiedersheim (55) says that they are present in the lizard and blindworm on the inner sides of the upper and lower jaws. Ihlder (17) has described the ending of nerve-fibres in the tongue of birds. He traced them into oval, concentric, club-shaped bodies, like those seen by Krause and Kölliker in the lingual papillæ of mammals.

#### THE TONGUE OF *MEPHITIS MEPHITICA*.

The tongue about to be described was taken from quite a young animal, and the following method was adopted in preparing it for histological examination. As soon as removed from the body it was placed in a mixture of five parts Müller's fluid and one part alcohol. After remaining in this mixture for ten days it was washed for thirty-six hours in running water, and then transferred to strong alcohol, where the har-

dening was completed. Subsequently portions of the organ were embedded in celloidin in the usual manner. My efforts to obtain sections stained with chloride of gold were not successful.

**General Description of the Tongue.**—The organ is 44 mm. long, 19 mm. wide, and 9 mm. in thickness. It is perfectly free for 15 mm. from the frænum, or a trifle more than one third of its length. Its length is therefore a little more than twice its width, which is quite uniform from the base to near the apex. Here it becomes thinner and somewhat elliptical in form. The upper surface is slightly convex posteriorly, and more or less flattened near the anterior extremity. There is a very slight raphé running forwards from the middle third of the tongue to its junction with the anterior third; here it takes the form of a shallow groove, which disappears just before reaching the tip. There is also a well-defined mesial groove at the posterior part of the dorsum, commencing midway between the two circumvallate papillæ, and running backwards for 10 mm. In the anterior third, beginning a little back from the apex, and reaching to the lateral margin, are four or five transverse ridges with corresponding depressions curving backwards, which give to this part of the tongue a corrugated appearance.

The upper surface, including the lateral margins in front of and lying between the circumvallate papillæ, is covered with tactile and mechanical papillæ, the points of which are directed backwards. These become gradually smaller as they approach the anterior extremity. The region of the tongue lying behind the gustatory area has projecting from its surface large cone-shaped papillæ, the apices of which are directed backwards and inwards. These increase in size, but decrease in number, as they recede towards the posterior limits of the organ.

Papillæ of the fungiform type are scattered quite uniformly over the dorsum and upon the sides of the middle third of the tongue, but terminate posteriorly in front of the area of the circumvallate papillæ. The average distance between them in this region is about 0.5 mm. They are very sparingly dis-

tributed to the anterior third, and are much smaller than those of the middle portion.

On each lateral half of the tongue is situated, near the anterior margin of the posterior third of the papillary surface, a large circumvallate papilla. These two papillæ lie in the same plane, and are 6 mm. apart. The left one is a little the larger of the pair. They are elliptical in form, and are placed at an oblique angle to the long axis of the tongue, with their anterior extremity directed outwards. Each papilla is encircled by a deep and rather wide trench, in which it is quite movable. Around the trench, and also forming part of its wall, are large conical-shaped papillæ. The larger of the two circumvallate papillæ measures, at its summit, 2 mm. in its long diameter, and 1.4 mm. in its short. The upper surfaces of both present an uneven or ridged appearance. No papilla foliata was found.

The under surface of the tongue is perfectly smooth except at the borders and tip, at which points are distributed numerous small tactile or mechanical papillæ. Anteriorly it is marked by a deep median groove, commencing at the frænum and running towards the apex. This becomes, however, rapidly superficial, and disappears altogether about 9.5 mm. from the tip.

The Circumvallate Papillæ.—These papillæ are distinctly lobate posteriorly; their upper and lateral contours are necessarily, therefore, somewhat uneven and irregular. Still, in some sections, I found the sides comparatively symmetrical. The diameter of the papilla at its base is always less than at the summit. In many sections the sides are vertical, or slightly oblique for about half their length, and then bend inwards and downwards.

The relation of the trench to the shape of the papilla is peculiar and, so far as I am aware, quite unusual (see figs. 2 and 3). Posteriorly, it is wide and deep, and passes directly beneath the papilla, thus giving it (the papilla), for about half its diameter, a free under surface.

Anteriorly and externally the trench becomes narrower

(though this is not constant) and more shallow. This pedunculated arrangement of the base of the papilla accounts for its free mobility, first noticed in the superficial examination. In some sections the trench is so extremely narrow that the surfaces of the opposing walls are almost contiguous. The width of the trench is usually greater in its upper portion, becoming, in most cases, gradually narrower as it curves downwards and inwards. The outer wall reaches nearly to the level of the upper surface of the papilla. Serous glands are present in the body of the papilla, but both mucous and serous glands (the latter being the more numerous) are very abundant in this region of the tongue. The ducts of the serous glands open into the trench, either at its sides or where it passes beneath the papilla. They are very plentiful. In one small horizontal section I counted twelve separate (?) ducts. Towards its upper part the papilla carries many secondary papillæ, the depressions between them being filled by epithelium. The nerves are mainly non-medullated. They form a network in the upper part of the papillary axis, from which branches radiate outward towards the lateral margins, terminating, apparently, at or near the bases of the taste-bulbs.

The taste-bulbs are very numerous in the circumvallate papillæ. They are distributed along the sides in a zone of ten or twelve tiers or rows, but are most thickly placed at the under surface of the papilla facing the bottom of the trench. The bulbs in this situation, although protected to a remarkable degree, are often smaller and less fully developed than elsewhere. I counted here, in one horizontal section, a group of forty-five on a surface 0.3 mm. square. The estimate of the number of these structures cannot be very exact. In one quarter of a horizontal section, made at the lower third of the papilla, I counted fifty-five bulbs. If we allow 200 in each tier, and allow ten tiers, we shall have 2000 bulbs for each papilla, or 4000 for the two. Bulbs are also present in the epithelium bordering the mid-trench (fig. 3) between the two large divisions of the papilla. In one section I met with them (fig. 3) on the free upper surface. I likewise found them in



the lower half of the outer wall of the trench. In some vertical sections they are arranged along the sides and lower surface in several rows.

The bulbs are quite irregular in size, and exhibit some variation in shape (fig. 5 shows the structure of the bulbs magnified 240 diameters. Their average length is about 0.06 mm.). The neck is very short and narrow, and only in a single bulb did I observe hair-like processes protruding through the pore. The nuclei of the peripheral cells stain quite deeply in hæmatoxylin. The outer layer of epithelium, at the point of its perforation by the bulbs, stains a uniform yellow in picro-carmin. I did not succeed in identifying gustatory as distinct from covering cells, though by teasing I was enabled to dislodge several bulbs from their position in the epithelium, and, in one case, to isolate a bulb with a nerve-fibril attached to or entering its base.

The Fungiform Papillæ.—These papillæ offer nothing very unusual in their general appearance. In shape they resemble the human type. A variation from the normal, however, is seen in their distribution, they being more numerous and larger over the middle of the dorsal surface than elsewhere.

In a few cases I found isolated taste-bulbs in the epithelium at the upper part of the papilla. The best specimen is represented by fig. 6. This papilla contains two bulbs, but they are neither of them of a high order. They are arranged obliquely near the summit, with their apices directed outwards and upwards, and measure about 0.05 mm. in length, and 0.032 mm. in breadth. In none of my sections do they appear to reach the surface of the epithelium.

Non-medullated nerve-fibres are quite abundant in the upper part of the body of the papilla, and nerve-fibrils can be seen running directly beneath the epithelium containing the taste-bulbs. Beyond this point I was unable to trace them. A few collections of ganglion-like cells are scattered along the course of the nerves. In some of the papillæ the nerve-fibres terminate in end-bulbs, as already pointed out by Krause and

Kölliker. Neither serous nor mucous glands were observed near the fungiform papillæ.

The tactile and mechanical papillæ are very numerous, covering the upper surface of the tongue from the base to the apex. They are largest at the posterior part of the dorsum (behind the gustatory structures), and diminish in size, but increase in number and density, as they approach the anterior extremity. One that I measured, from the posterior part of the dorsum, was 1·8 mm. in height. About the middle of the tongue I counted twenty-five on a square millimetre of surface. Here they are 0·25 mm. in height. They present considerable variation in shape. Anteriorly they are flattened, or slightly convex on the top, with their sides vertical, forming either a right angle with the upper surface, or having their upper edges slightly rounded. Occasionally the sides are prolonged upwards for a short distance, terminating in spiniform processes. Interspersed among these papillæ, but chiefly confined to the gustatory area and posterior surface, are a few cone-shaped ones, the points of which are directed backwards and inwards. Each papilla is usually seated upon two papillary upgrowths of the mucosa. The free surface is covered with a thick layer of cornified epithelium, which, in the cone-shaped, papillæ, presents an imbricated arrangement. In their internal structure these papillæ do not differ materially from ordinary conical papillæ.

It is probable that the cone-shaped papillæ of the anterior and middle dorsal surface of the tongue are mechanical rather than tactile in function.

On the posterior surface of the epiglottis, near the line of union of the first and second fourth, I noticed in the stratified pavement epithelium a few isolated bulb-like structures. I did not, however, meet with them below this point. In the same region, on the right side, I found the bulb-like structure shown in figure 7. It will be seen at once that it is entirely subepithelial in position and structure. It occupies a cavity of the mucosa, with its apex resting against the base of the deep layer of columnar cells of the epithelium. Its length is

about 0.045 mm., and its greatest transverse diameter about 0.025 mm.

I examined a very large number of sections of the soft palate and uvula, but did not succeed in finding any bulb-like structures.

To sum up briefly in conclusion, there are situated at the posterior part of the tongue of *Mephitis* two large circumvallate papillæ. Upon superficial examination the most striking features are their size, the ridged appearance of their upper surface, and their rather unusual shape. Under the microscope each papilla is seen to be divided posteriorly into two unequal lobes or divisions, and to have in the same region a free under surface, the trench passing directly beneath its base, thus affording great protection to the bulbs occurring here. Anteriorly the papilla is connected with the tongue by a pedicel-like attachment.

The taste-bulbs of the circumvallate papillæ are very numerous, especially in the epithelium of the under surface, and offer considerable irregularity in shape, size, and distribution. A few bulbs occur in the epithelium of the upper surface of the papillæ, and in that of the outer wall of the trench. In a single instance I observed a bulb with a nerve-fibril attached to its base. Glands of the serous and mucous types are very abundant, but the former are chiefly limited to the gustatory area of the tongue. Serous glands are also met with in the papillary body itself.

A few fungiform papillæ possess isolated bulbs lying in the epithelium at their summit, and they also occur in the upper part of the posterior surface of the epiglottis; but in both these regions they are primitive in character and position.

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## EXPLANATION OF PLATE XI,

Illustrating Mr. Frederick Tuckerman's paper on "The Tongue and Gustatory Organs of *Mephitis mephitica*."

FIG. 1.—Vertical section through the right circumvallate papilla. *S. P.* Secondary papillæ. *t.* The trench. *r.* Section through the ridge which surrounds the trench. *t. b.* The taste-bulbs arranged in tiers. *gl. d.* The ducts of the serous glands, opening into the bottom of the trench. *m. m.* Mucous membrane. ( $\times 20$  times.)

FIG. 2.—Vertical section through the same circumvallate papilla. *S. P.* Secondary papillæ. *t.* The trench. *r.* Ridge. *C. P.* Conical papilla, somewhat depressed. *t'.* The trench passing beneath the papilla, showing the arrangement of the taste-bulbs in the epithelium of the under surface. *gl. d.* The ducts of the serous glands. ( $\times 24$  times.)

FIG. 3.—Vertical section through the posterior part of the same papilla. *t.* The trench. *t. b'.* Taste-bulbs in the epithelium of the upper surface. *m. t.* The mid-trench, partly separating the papilla into two divisions. *gl. d.* Ducts of the serous glands. ( $\times 20$  times.)

FIG. 4.—Vertical section through the anterior part of the same papilla. *t. b.* Taste-bulbs, divided at right angles to their long axis. *gl. d.* Ducts of the serous glands. ( $\times 30$  times.)

FIG. 5.—Vertical section through the base of the same papilla, showing the bottom of the trench and the six lowest tiers of taste-bulbs. *t.* The trench. *t. b.* Taste-bulb. *g. p.* Gustatory pore. *s. e.* Stratified epithelium. *o. l.* Outer layer of stratified epithelium. *gl. d.* The ducts of the serous glands. *m. m.* Mucous membrane. ( $\times 240$  times.)

FIG. 6.—Vertical section through a fungiform papilla, from the group in front of the circumvallate papillæ. *t. b.* Taste-bulbs. *p. p.* Papillary processes. *s. e.* Stratified epithelium. ( $\times 220$  times.)

FIG. 7.—Transverse vertical section through the upper part of the posterior surface of the epiglottis. *f. s.* Free surface of the stratified pavement of epithelium. *d. l.* Deep layer of columnar cells of the epithelium. *b. l. s.* Bulb-like structure lying in the mucosa, with its apex touching the base of the cells of the deep layer of epithelium. *m. m.* Mucous membrane. ( $\times 240$  times.)





On the Quadrate in the Mammalia.<sup>1</sup>

By

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IN what skeletal piece in the Mammalia is the quadrate of the Sauropsida and Ichthyopsida to be looked for? is a question which has received very varied answers.

During the last few years several works have appeared which attempt to answer this question, and that in a new way. There are several by Albrecht,<sup>2</sup> and one by Dollo.<sup>3</sup>

I will first of all set myself to discuss shortly Albrecht's researches.

He brings forward the various views as to the mode of

<sup>1</sup> Translated by Wm. B. Benham, B.Sc., from the 'Biolog. Centralblatt,' vi, (1886), pp. 648—658.

<sup>2</sup> P. Albrecht, 'Sur la valeur morphologique de l'articulation mandibulaire, du cartilage de Meckel et des osselets de l'orice, avec essai de prouver que l'écaille du temporal des mammifères est composée primitivement d'un squamosal et d'un quadratum,' Bruxelles, 1883.

Ibid. 'Sur le crâne remarquable d'une idiote de 21 ans,' Bruxelles, 1883.

Ibid. 'Sur la valeur morphologique de la trompe d'Eustache, et les dérivés de l'arc palatin, de l'arc mandibulaire, et de l'arc hyoïdien des vertébrés,' Bruxelles, 1884.

Extracts from these works are found in :

P. Albrecht, "Ueber den morphologischen Werth der Gekörknöchelchen und des Unterkiefergelenkes der Wirbeltiere," 'Official Report of the Fifty-sixth Meeting of German Naturalists and Doctors,' Freiburg, 1884, p. 143.

Ibid. "Ueber den morphol. Werth des Unterkiefergelenkes, der Gehörknöchelchen, und des mittlern, und äussern Ohres der Säugetiere." 'Report of the Third International Otological Congress at Basel, 1884,' Basel, 1885, p. S.

<sup>3</sup> L. Dollo, "On the Malleus of the Lacertilia and the Malar and Quadrate Bones of Mammalia," 'Quart. Journ. Mic. Sci.,' October, 1883.

articulation of the lower jaw of Vertebrates, and groups them in the following table:

Articulation of the Lower Jaw in Vertebrates, except Mammals.	Articulation of the Lower Jaw in Mammals.
Quadrato-articulare articulation.	Squamoso-articulare (Huxley). Squamoso-dentary (Gegenbaur, Kölliker, Wiedersheim).

Consequently, whilst Huxley assumes the lower jaw of the lower Vertebrates to be homologous with that in the Mammalia, Gegenbaur, Kölliker, and Wiedersheim see in the lower jaw of Mammals only the dentary piece of that in the remaining Vertebrates.

In the next table Albrecht sets forth the various views as to the development of the auditory ossicles in the Mammalia.

	I.—Visceral Arch.	II.—Visceral Arch.	Auditory Canal.
Reichert	Malleus . incus	Stapes	...
Günther	Malleus . incus . stapes	...	...
Gegenbaur {	Malleus=articulare { Incus =quadrate {	Os lenticulare (symplectic) Stapes=hyomandibular	} ...
Huxley . .	Malleus=quadrate	Incus =hyomandibular, os lenticulare, stapes	...
Parker . .	"	Incus ="hyomandibular	...
Parker . }	" {		Stapes.
Bettany . }	" {		
Salensky			
1st Theory	Malleus . incus . stapes	...	...
Salensky			
2nd Theory	Malleus . incus	...	Stapes (outside the periarterial tissue).
Kölliker. {	Malleus=articulare { Incus =quadrate {	...	Stapes.
Wiedersheim	"	...	...
Fraser . .	Malleus	Incus=os lenticulare	Stapes " (outside the periarterial tissue).

<sup>1</sup> A. Fraser, "On the Development of the Ossicula auditus of the Higher Mammalia," 'Phil. Trans.,' vol. 173, part iii, 1882.

Gegenbaur, Kölliker, Wiedersheim, therefore, regard the malleus as the articulare, and the incus as the quadrate.

Huxley, Parker, and Bettany look upon the malleus as the quadrate and the incus as the hyomandibular.

The incudo-malleolar articulare articulation, therefore, is to the former zoologists a quadrato-articulare articulation, and to the latter it is a hyomandibular-quadrato articulation.

Albrecht espouses neither the one view nor the other, and arrives, by his reasoning, at the result that in all Vertebrates the lower-jaw articulation is the same, viz. a quadrato-articulare articulation. He then reviews the relations of the auditory ossicles. In the Sauropsida, Cœcilia, and Urodela there is a columella. It commences at the tympanic membrane and ends at the "membrana ovalis" (as Albrecht names the membrane which closes the fenestra ovalis). In the Anura four more or less ossified pieces of cartilage are found in the same position; these four pieces of cartilage are homologous with the columella. In the Mammalia the malleus touches the tympanic membrane; the stapes reaches the fenestra ovalis. Therefore Albrecht concludes, "the columella is homologous with the row of auditory ossicles in the Mammalia. The columella unquestionably forms the suspensorium of the lower jaw. The malleus of the Mammalia belongs to the extra-mandibular portion of Meckel's cartilage, but this portion is homologous with the symplectico-articular ligament of the Amphibia and Sauropsida, therefore the suspensorium of the lower jaw is the same as in all the Vertebrates.

If, now, the articulation of the lower jaw in Mammals is homologous with that in the rest of the Vertebrates, in which a quadrato-articular articulation is present, then the quadrate must be looked for in that part of the Mammalian skull with which the lower jaw articulates. This, in the Mammalia, is the squamosal: consequently the quadrate of the Sauropsida and Ichthyopsida must be comprised in the squamosal.

Albrecht, indeed, finds in a newborn child affected with double harelip and double "Wolfsrachen," that this squa-



mosal is divided into two portions: the zygomatic process and the "scale." In the zygomatic process Albrecht sees the quadrate of the rest of the Vertebrates. He finds the same conditions in a newborn horse, and in the squamosal of the right side of an idiot twenty-one years old.

Dollo uses the same arguments: first recapitulates Albrecht's results, and then describes his own researches. He asks the question: Is it possible that the quadrate can form a part of the interfenestral chain of auditory ossicles? If we succeed in finding a Vertebrate in which the lower jaw consists of the six normal elements, and in which, moreover, a true quadrate and a malleus are present, then it is impossible that the quadrate can be homologous with any of the auditory ossicles. Therefore—

(1) It cannot be compared with the malleus, since this is present, and (2) it would be impossible to identify it with one of the remaining auditory ossicles, because it would be outside the malleus, and touch none of the other auditory ossicles.

It depends, therefore, on finding a malleus which shall fulfil the above conditions. Dollo maintains that he has found in many Lacertilia (*Leiolepis*, *Uromastix*, and their allies) a skeletal piece which has the morphological value of a malleus.

Dollo's arguments in support of this are:

1. The piece has the form of a malleus, and all the characteristic parts of one can be distinguished.

2. The piece has the same connections: it is fixed to the tympanic membrane in such a way that the manubrium is parallel to the membrane. At the side, in the region of the cervix, it is connected by cartilage with the rest of the auditory ossicles; and with the quadrate it stands in the same relation as the malleus of Mammals with Albrecht's "quadrate."

3. It is connected with the articulare of the lower jaw by a malleo-articulare ligament—Albrecht's extra-mandibular portion of Meckel's cartilage.

4. It can scarcely be doubted that this malleus is identical with that described by Peters for the crocodiles.

5. The malleus in the Mammalia serves for the insertion of the tensor tympani: the same, according to Parker, should be the case with the "malleus" of the Lacertilia.

These are Dollo's arguments, and he concludes in the following terms: "I believe, therefore, that I have found in the Lacertilia a true malleus, which is homologous with that of the Mammalia, and that we have a support for Albrecht's theory. The columella of the Sauropsida, therefore, will not be homologous with the malleus and incus, and articulare and stapes, but, as Albrecht thinks, only with the three last pieces. Albrecht later denoted the homology of these three pieces by the name "Columellina."

Let us now subject Albrecht's work to a short examination. First of all, it must be remarked, that his view—that the quadrate of the Sauropsida is homologous with the zygomatic process of mammals—is not absolutely new. Indeed, in 1810, Tiedemann says, in his well-known work, '*Anatomie und Naturgeschichte der Vögel*,' vol. i, p. 191, "The two quadrate bones of birds are analogous with the articular region of the squamosal of man and mammals, namely, with the glenoid fossa, the glenoid process, and the zygomatic process of the squamosal, which have become detached from the squamosal as a separate bone." Further, Platner<sup>1</sup> upheld this view in the most decided manner.

Köstlin<sup>2</sup> is also of this opinion.

Again, the possibility of the separating of the zygomatic process from the scale of the squamosal was recognised before Albrecht. Duvernoy adduced an instance of this sort in the second edition of Cuvier's '*Leçons d'Anatomie Comparée*,' vol. iv, p. 98: "We are led to compare the quadrate bone to that portion of the temporal which furnishes the glenoid fossa, and we base this comparison on the fact that this portion of the temporal is separated from the petrous and

<sup>1</sup> F. Platner, '*Bemerkungen über das Quadratbein und die Paukenhöhle der Vögel*,' Dresden and Leipzig, 1839.

<sup>2</sup> O. Köstlin, '*Der Bau des Knöchernen Kopfes in den Vier Klassen der Wirbelthiere*,' Stuttgart, 1884, pp. 212, 213.

periotic, as well as from the scale of the temporal, in a skull of *Hydrochærus*, which we have under observation."

Thus Duvernoy, more than forty years ago, partly on the same grounds as Albrecht, arrived at the same conclusion as he did.

I now turn to Dollo's researches. He says: "It is sufficient for me to find in *Uromastix* and its allies a malleus, which is homologous with that of the *Mammalia*."

Unfortunately, I cannot grant to Dollo the right of having just discovered this fact. This belongs to Peters,<sup>1</sup> who had, indeed, nearly ten years previously, found this, and very distinctly, in *Uromastix*.

Afterwards, Peters pointed out that in *Sphenodon* a true malleus is present, which Huxley<sup>2</sup> had interpreted as the outer stapes-cartilage.

Peters says, on pages 43, 44 of his paper: "For the purpose of this research I availed myself, for comparison, of an example of *Uromastix spinipes* from Egypt; in this reptile, the relation of the cartilage, described by me as a malleus, with the lower jaw or Meckel's cartilage, remains so very distinct without any preparation that anyone will easily be able to form an opinion on the point in question by simply examining this very common form, which ought scarcely to be absent in any collection. When the head has been removed the stapes will readily be seen lying exposed, in the same way as in *Sphenodon*, by the side of the exoccipital bone. But in *Uromastix* it does not lie so near this bone as in *Sphenodon*, and especially at its outer end, where it passes round under the inner edge of the quadrate bone to unite itself in an articular pit, with the head of the cartilaginous malleus. The body of the malleus consists of a cylindrical piece, which fixes itself at the tympanum, and here ends in a small plate, the longer part of which is directed forwards, whilst the shorter end approaches

<sup>1</sup> W. Peters, "Über die Gehörknöchelchen und ihre Verhältniss zu den ersten Zungenbeinbogen bei *Sphenodon punctatus*," 'Monatsber. d. k. preuss. Akad. d. Wiss.,' Berlin, 1874, p. 40.

<sup>2</sup> "On the Malleus and Incus, &c.," 'Proc. Zool. Soc.,' Lond., 1869.

the edge of the 'mastoid' bone. But at the point where the malleus is connected with the stapes, there springs at right angles to it, downwards and forwards, a longer process (*processus longus mallei*), which descends along the inner side of the quadrate, passing between it and the hinder end of the pterygoid and becomes tendinous in front of the inner edge of the articular cavity of the lower jaw, into which it sinks."

Peters gives drawings of these relations. That this work by Peters should escape Dollo is so much the more strange, since Balfour, in his '*Comparative Embryology*,' vol. ii, p. 483 (foot-note), cites him, and Hoffmann, in his '*Reptilia*' (Bronn's '*Klassen und Ordnungen des Tierreichs*'), p. 605, not only gives Peters's contribution verbally, but also copies his figures.

Moreover, this is not the only work by Peters in which the view that the Sauropsida possess a malleus homologous with that of the Mammalia is upheld. Indeed, in the work quoted by Dollo,<sup>1</sup> Peters speaks very decidedly on this point.

He found in a young alligator, with a head 13 cm. in length, a cartilaginous thread lying in a membranous sheath, which proceeds from Meckel's cartilage of the lower jaw through the aperture which exists at the hinder inner part of the upper surface of the quadrate. This thread he not only traced to the hinder border of the tympanic membrane, but also convinced himself that it is in connection with the cartilaginous plate, which is bent inwards by its narrow middle part towards the columella, the outer end of which is articulated with it. This cartilaginous plate, Peters insists, is nothing but the malleus, as, indeed, Breschet had interpreted it in birds.

Peters was able to see these relations still more clearly in an embryo crocodile of 70 mm. in length. The same condition of things was also found in an ostrich embryo. On p. 595 Peters expresses himself very decidedly and clearly: "In view of the observed facts the view that the articular portion of the

<sup>1</sup> W. Peters, "Ueber die Gehörknöchelchen und den Meckel'schen Knorpel bei den Krokodilen," '*Monatsber. d. k. preuss. Akad. d. Wiss.*,' Nov., 1868, p. 592.



lower jaw and the quadrate of Amphibia are homologous with the malleus and incus of the Mammalia loses every foundation."

In a later communication ("Ueber der Gehörknöchelchen der Schildkröten, Eidechsen, und Schlangen," 'Monatsber. d. Berl. Akad.,' January, 1869) Peters states that in an embryo of *Hemidactylus* the cartilaginous thread passing from the malleus bends round close to the quadrate, and sinks into the lower jaw. Therefore Peters recognised the malleus in the *Sauropsida* long before Dollo.

I pass now to my own researches on the subject. As is well known, the theory is to-day nearly universally taught, especially in England, that the columella "and its appendices" are modifications of the second, and not of the first, visceral arch. Thus Parker<sup>1</sup> has lately written, "After long years of labour and much vacillation of mind on the matter, I am now quite satisfied that the stapes, a little stirrup-bone of the ear-drum, is the uppermost element of the second or hyoid arch."

To these views Huxley's<sup>2</sup> researches on the stapes of *Sphenodon* especially contributed.

According to Huxley the hyoid cartilage rises up behind the quadrate till it has nearly reached the skull, and then appears suddenly to be bent in the form of a small scroll with a posterior concavity. This scroll is due to the widening out of the hyoid bone, which forms a cartilaginous plate. On the inner side this plate is produced into the stem (base) of the stapes, and soon ossifies. According to Huxley, therefore, the upper stapes-cartilage is nothing else than the inner end of the hyoid arch. The stapes and its appendices belong absolutely to this arch, and have nothing whatever to do with the mandibular arch.

On the other hand, Peters says: The connection of the hyoid arch with the stapes-cartilage (malleus) is not a primary but

<sup>1</sup> W. K. Parker, 'On Mammalian Descent,' London, 1885, p. 43.

<sup>2</sup> T. H. Huxley, "On the Representatives of the Malleus and Incus of the Mammalia in the other Vertebrates," 'Proc. Zool. Soc.,' London, 1869, p. 391.

a secondary condition. The hyoid arch applies itself to the malleus, is bound to it by connective tissue, and perhaps even fuses with it. The fibres of the hyoid arch are soft, and have a different direction from those of the stapes-cartilage (malleus), the harder fibres of which cross those of the hyoid arch. The swelling of the hyoid arch at the point where it joins the outermost part of the malleus is only apparent, arising not from the cartilage but from the connective tissue. According to Peters, the hyoid bone is, indeed, not connected with the inner process of the malleus, but passes below it, without adhering to it, so that the space between the outer and inner parts of the malleus is not, as Huxley thought, transformed into a foramen by a junction. According to him there is no doubt that at earlier stages Meckel's cartilage is connected with this inner hatchet-shaped process of the malleus by means of a fibre passing along the inner side of the quadrate.

According to Peters, therefore, the stapes-cartilage, i. e. the malleus of *Sphenodon*, is derived from the first visceral arch.

It is seen that the opinions on this very important point are very various. It is strange that Parker, too, in his many works on the development of the skull in Vertebrates, makes no mention of this work by Peters. Besides Hoffmann, Balfour mentions this point. He says (l. c., p. 483), "The strongest evidence in favour of Huxley's and Parker's view of the nature of the columella is the fusion in the adult *Sphenodon* of the upper end of the hyoid with the columella (Huxley). From an examination of a specimen in the Cambridge museum I do not feel satisfied that the fusion is not secondary, but I have not been able to examine the junction of the hyoid and columella in section."

Balfour was inclined to adopt Peters's view: I can do the same. In fact, Peters is right. The malleus (stapes-cartilage) is not derived from the hyoid arch: the connection with it is secondary: the malleus of *Sphenodon* and all Sauropsida is a derivative of the first visceral arch.

My material consisted of three specimens of *Sphenodon*, preserved in alcohol: for two of these (*a* and *b*), from the Museum of Yale College, I have to thank Mr. O. C. Marsh; the third (*c*) came from Prof. B. G. Wilder, of Ithaca. The specimen *a* measured about 360 mm., the tail being regenerate; *b* measured 290 mm., and *c* 210 mm. In the specimen *a* I have dissected out on both sides the part concerned, of *b* and *c* only that of the right side. Examined with a lens the hyoid arch is seen to be close to the cartilaginous part of the stapes; in fact, was in part fused with it. In order to be quite certain of this, series of sections from the preparations of *a* and *b* were prepared. These show that the hyoid arch is free from the real malleus, although it applied itself closely to the front edge of the stapes-cartilage. The relations in section are, certainly, not so distinct as I had expected; and the examination of *Sphenodon* alone had made the settlement of the point impossible. But that the hyoid has, in fact, nothing to do with the stapes is very clearly seen in *Tarentola annularis* (*Platydictylus ægyptiacus*). Here the hyoid arch is just as perfect as in *Sphenodon*, but it does not enter into so intimate a connection with the stapes-cartilage. From the long process of the malleus ("infrastapedial" of Parker), however, there passes downwards a thin fibre, to sink into the lower jaw; this is the epimandibular portion of Meckel's cartilage ("ceratohyal" of Parker). Here, therefore, we have a similar condition to that described by Parker<sup>1</sup> for the crocodile.

From the observed facts, there is no doubt that the malleus of *Sphenodon*, and therefore of all the Sauropsida, is not derived from the hyoid arch, but from the mandibular arch. Albrecht<sup>2</sup> has already maintained on logico-theoretical grounds, that the wrongly so-called hyomandibular (ceratohyal) is nothing else but the dorsal portion of the first visceral arch, that is of Meckel's cartilage. My own researches on *Sphenodon*, and

<sup>1</sup> W. K. Parker, "On the Structure and Development of the Skull in the Crocodilia," 'Trans. Zool. Soc.,' vol. xi, 1883, pl. 68, fig. 19.

<sup>2</sup> P. Albrecht, 'Sur la valeur morphologique de la trompe d'Eustache,' Bruxelles, 1884.

more especially on *Gecko*, strengthens this view. In both the hyoid arch is complete, but has absolutely nothing to do with the malleus. But the proof that the hyomandibular is equivalent to the epimandibular adds strength to Albrecht's other hypothesis, that the quadrate originally belonged to the palatine arch and not to the mandibular arch.

I will now speak of the quadrate itself. That it cannot be looked for in one of the auditory ossicles follows clearly from the foregoing.

According to Tiedemann, Platner, Köstlin, Duvernoy, and Albrecht, the quadrate of mammals is equivalent to the zygomatic process of the squamosal. I agree fully with this view. To the examples adduced by Albrecht and Duvernoy of an actual separation I can add a further one. In a stillborn tiger I found in the right squamosal very much the same condition of things as Albrecht has described in the skull of a newborn child. The zygomatic process is separated by a "suture," which nearly passes through the whole scale.

In the upper part we have the true squamosal, in the lower we see the quadrate. All these separations in the "squamosal" must be considered as atavistic. That they are so without doubt results from Cope's researches on the Pelycosauria of the Permian formation. Cope looks upon these reptiles as the ancestors of the mammals. I have in another place ('*Morphol. Jahrbuch*') endeavoured to show that these are somewhat too specialised to answer this hypothesis, but that they are very closely allied to the ancestors of the Mammalia. I give Cope's<sup>1</sup> remarks on the quadrate of these interesting forms in his own words: "Although the malar bone is out of place in the specimen described, examination of the skull of *Clepsydrops natalis*, where it is preserved in position, shows that this horizontal ramus of the quadrate is nothing more than the zygomatic process of the squamosal bone of the Mammalia forming with the malar bone the zygomatic arch."

<sup>1</sup> E. D. Cope, "The Relations between the Theromorphous Reptiles and the Monotreme Mammalia," '*Proc. Amer. Assoc. Adv. Sci.* (1884, Philadelphia), vol. 33, p. 473.



I myself think that there is no doubt that the quadrate of the lower Vertebrates is contained in the zygomatic process of the mammals.

According to Albrecht and Dollo, the quadrato-jugal is contained in the malar (jugal). From what I find in a very young skull of *Dasypus*, the truth of this assertion appears to me doubtful. In this skull I find, on both sides, a perpendicular fissure which tends to separate the articular surface of the process together with the jugal. I think that this half-separated piece represents the quadrato-jugal of the Sauropsida; to myself, therefore, it appears as probable that this quadrato-jugal is included in the quadrate, an assumption which is supported by the conditions found in *Sphenodon*. Here, in older specimens, the quadrato-jugal is fused with the quadrate, while it is free in the young form.

The results of these observations I will summarise as follows:

1. The assertion, put forward by Breschet and Peters, and again by Dollo, that the cartilaginous distal portion of the columella (stapes) of the Sauropsida is homologous with the malleus of the Mammalia, is true.

2. The malleus in the Sauropsida and the Mammalia belongs to the first and not to the second visceral arch, that is, to the epimandibular portion of Meckel's cartilage.

3. The so-called hyomandibular or ceratohyal of Sauropsida is nothing else than the epimandibular portion of Meckel's cartilage (Peters, Albrecht, Baur).

4. The "quadrate-cartilage" really belongs, not to the mandibular, but to the palatine arch. (Albrecht asserted this.)

5. The homology, asserted by Tiedemann, Platner, Köstlin, Duvernoy, Albrecht and Cope, between the quadrate of the Sauropsida and the zygomatic process of the squamosal, is true.

6. Probably the anterior end of this process represents the quadrato-jugal.

## On the Hæmoglobin Crystals of Rodents' Blood.

By

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THE crystals of hæmoglobin since their first discovery have been described by various observers as occurring in no less than five out of the six crystallographic systems. Subsequent investigators have reduced this number to two, namely, the rhombic system, in which the hæmoglobin from the blood of most animals crystallises; and the hexagonal system, in which that from the blood of certain rodents is said to crystallise.

This research was undertaken at Professor Lankester's suggestion, in order, first, to ascertain whether these six-sided crystals really belonged to the hexagonal system; and, secondly, to find, if possible, an explanation of the difference of crystalline form that hæmoglobin presents in different animals, while in its other chief properties hæmoglobin is universally the same.

It will be convenient to take the subject under the following heads:

1. Historical.
2. Hexagonal blood-crystals.
3. Influence of the other constituents of the blood on the crystalline form of hæmoglobin crystals.
4. The crystalline forms of hæmoglobin obtained by mixing the blood from different animals.
5. Can squirrel's hæmoglobin be obtained in any form other than hexagonal crystals?
6. Conclusions and remarks.

## 1. Historical.

Oxyhæmoglobin crystals were first described by Reichert<sup>1</sup> as occurring in the uterus of a pregnant guinea-pig; by Leydig<sup>2</sup> as occurring in the alimentary canal of the leech; and by Kölliker,<sup>3</sup> obtained from the blood of the dog, python, and other animals. Kölliker considered the crystals to be composed of a more or less modified hæmatin. Funke<sup>4</sup> was, however, the first to make complete observations upon them, and to recognise their true nature. Kunde,<sup>5</sup> working at the same time, made extensive observations from a comparative point of view, and was the discoverer of the exceptional form of the crystals in the guinea-pig and squirrel. Since then many investigators have worked at the subject, notably Lehmann,<sup>6</sup> Rollett,<sup>7</sup> von Lang,<sup>8</sup> and Preyer,<sup>9</sup> in whose exhaustive treatise a complete bibliography of the subject up to 1871 is given.

Our present knowledge of the crystalline form that hæmoglobin assumes may now be summarised as follows:

a. In the great majority of animals<sup>10</sup> in which hæmoglobin

<sup>1</sup> Reichert, 'Müller's Archiv,' 1849, p. 197.

<sup>2</sup> Leydig, 'Zeitsch. f. wiss. Zool.,' Bd. i, 1849, p. 116.

<sup>3</sup> Kölliker, 'Zeitsch. f. wiss. Zool.,' Bd. i, 1849, p. 266.

<sup>4</sup> Funke, 'Zeitsch. f. nat. Med.,' N. F., Bd. i, 1851, p. 184; Bd. ii, 1852, p. 204 and p. 288. "De sanguine venæ livæ," 'Diss. Lipsiæ,' 1851.

<sup>5</sup> Kunde, 'Zeitsch. f. nat. Med.,' N. F., Bd. ii, 1852, p. 276.

<sup>6</sup> Lehmann, 'Ber. d. k. Säch's Ges. d. Wissen.,' 1852, p. 22.

<sup>7</sup> Rollett, 'Sitzungsber. d. Wien. Akad.,' Bd. xlv, 1862, p. 65.

<sup>8</sup> Lang, *ibid.*

<sup>9</sup> Preyer, 'Die Blutkrystalle,' Jena, 1871.

<sup>10</sup> To the animals falling under this rule I can add several, the crystalline form of the hæmoglobin of which have not been hitherto recorded. I am much indebted for specimens of the blood of these animals to my friend Mr. F. E. Beddard, of the Zoological Gardens.

Opossum (*Didelphys cancrivora*).—Very large and dark red crystals, can be readily obtained. They belong to the rhombic system.

Kangaroo (*Macropus giganteus*).—Crystals are more soluble, and so less readily obtained. They are rhombic prisms, slenderer than in the opossum.

occurs, vertebrate and invertebrate, crystals of it can be obtained in the form of prisms and plates belonging to the rhombic system.

b. The exceptions to this rule hitherto noted are the following :

i. Guinea-pig. Hæmoglobin crystals from the blood of this animal are tetrahedra, once supposed to belong to the regular system, but now shown by von Lang to be in reality rhombic.

ii. Lehmann mentions that similar tetrahedra may be obtained from the blood of the mouse and rat. This has not since been confirmed.

iii. In several birds the crystals obtained are also tetrahedra.

iv. In three animals—the squirrel, the hamster, and the mouse—six-sided plates have been described.

v. In one of these, the hamster, rhombohedra are described as occurring also.

## 2. Hexagonal Blood-crystals.

We will take the three animals in which the hæmoglobin is said to crystallise in the hexagonal form one by one.

a. Squirrel.—The discovery of the fact that hæmoglobin crystals from this animal are six-sided plates was made by Kunde (1852). Writing in the same year, Lehmann asserts that though these crystals are six-sided they do not belong to the hexagonal system. He gives, however, no reasons for this assertion. Lang and Preyer arrived at the opposite conclusion i. e. that they do belong to the hexagonal system, from the study of their optical properties.

*Belideus breviceps* (a marsupial).—Crystals similar to those of the opossum.

Seal (*Phoca vitulina*).—Rhombic prisms, many of them very short and simulating hexagons. Easily obtained.

Bear (*Ursus syriacus*).—Bunches of rhombic needles, easily obtained. They are slenderer than those obtained from dog's blood as a rule, some being almost silken in appearance.

*Hydromys leucogaster* (white-bellied beaver rat).—Rhombic prisms.

*Sus leucomystax* (white-whiskered swine).—Rhombic prisms.

Water-vole (*Arvicola aquatica*).—Crystals are obtained easily by adding water to the blood. They are of the usual rhombic shape.



My own observations are as follows:—The crystals can be obtained with the greatest ease by simply adding a drop of water to a drop of defibrinated blood on a slide, and covering it; in less than a minute crystals appear. I have also prepared them by other methods;<sup>1</sup> but in all cases the crystalline form is the same. When first formed the crystals are six-sided plates, many equilateral, but many not. After recrystallisation, however, the crystals are then all but perfectly regular. The question then arises, Do they belong to the hexagonal system or not? To this question one of the three following answers must be the correct one.

1. They do belong to the hexagonal system.

2. They do not belong to the hexagonal system, but are rhombic crystals, having a so-called “hexagonal habit.” In mineralogy instances are known of such occurrences. This is the case with copper-glance, some of whose crystals so closely resemble hexagonal ones that several mineralogists believed that there were two kinds, one being hexagonal. Again, mica is an instance of a monoclinic crystal with “hexagonal habit.”

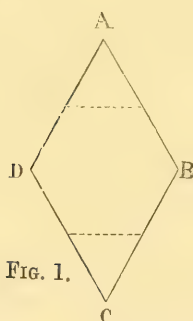


FIG. 1.

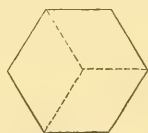


FIG. 2.

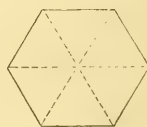


FIG. 3.

Suppose A B C D (fig. 1) to be the basal plane of a rhombic plate, and the angle A B C to be approximately  $120^\circ$ , the lines

<sup>1</sup> The method that I have found best for the preparation of blood-crystals in most animals is to add to defibrinated blood a sixteenth of its volume of ether, and then to shake for two or three minutes until the liquid becomes of a clear lake colour; in the course of time, varying from five minutes to three days, crystals form in abundance (‘Gamgee’s Physiological Chemistry,’ p. 87)

joining  $A C$ ,  $B D$  being the axes. Then if the angles  $D A B$ ,  $D C B$  be replaced, as shown by the dotted lines, a hexagon will be produced differing but little from a regular hexagon.

3. The third alternative is that they may belong to the rhombic system by being twins, consisting of three parallelograms or six triangles, as is shown in figs. 2 and 3. Twins are, however, rare in the rhombic system.

In order to settle this question it is necessary to examine the optical properties of the crystals.

Crystals may be divided, according to their optical properties, into three classes :

1. *Isotropic*.—Those in which there is no distinction of different directions as regards optical properties. This includes crystals belonging to the regular system. They have but one refractive index, i. e. refract light like amorphous bodies do, singly.

2. *Uniaxal*.—Those in which the optical properties are the same for all directions equally inclined to one particular direction, called the optic axis, but vary according to this inclination. This class includes crystals belonging to the dimetric system (crystals with three rectangular axes, two of them being equal) and the hexagonal system. The optic axis corresponds with the principal crystallographic axis. In the direction of this axis a ray of light is refracted singly, and in other directions doubly.

3. *Biaxal*.—This includes the remaining three systems of crystals, the trimetric or rhombic (three rectangular axes all unequal), the monoclinic, and the trichinic. In these there are always two directions along which a ray is singly refracted.

The best test, as to whether a substance is doubly refractive or not, is this : If between crossed nicols, which consequently appear dark, a substance be interposed that makes the darkness give place to illumination, however feeble, that substance is doubly refractive. This action is termed the depolarisation of the ray.

The crystals of squirrel's hæmoglobin I submitted to this

test, with the result that no depolarisation of the light can be detected, when they are examined with the apparent basal plane perpendicular to the axis of the instrument and rotated; nor when a quartz plate is inserted do they produce any modification of the tint, as the stage is turned. The instrument used was a Zeiss polarising microscope.

Hence the presumption is that they belong to the hexagonal system, as rhombic crystals with hexagonal habit or rhombic twins would produce some double refraction examined in this way.

I submitted the question as to whether this was conclusive to Professor Lewis, of Cambridge, and he kindly wrote to me in answer as follows:

“The observation under the microscope between crossed nicols, so far as it goes, is rather in favour of the crystals being hexagonal, that is, presupposing that the field remains dark when the crystal is rotated in the field of view. However, this is not quite conclusive, and in such cases greater certainty would be obtained if the crystals were placed under a Bertrand’s polarising microscope, to see the shape of the interference rings and cross.”

It should be here stated that uniaxal crystals in the direction of their optic axis exhibit a symmetrical cross and circular rings; in biaxal crystals the rings are oval, or at any rate not circular, and the cross is not symmetrical. This is the case, because the resistance to displacement in the three cardinal directions called the axes of elasticity are all unequal in biaxal crystals. This is true, not only for the crystalline substance itself, but also for the luminiferous ether that pervades it.<sup>1</sup>

Acting on Professor Lewis’s advice, I submitted the crystals to Professor Judd, who with Mr. Fletcher’s co-operation examined them, and gave me the following report, for which I am much indebted to him:—“I have every reason to believe the crystals belong to the hexagonal system from their form, and their extinction between crossed nicols. I regret, however,

<sup>1</sup> The cardinal directions are, however, believed not to be the same for the ether as for the material of the crystal.

to find that their minute size, and especially their extreme tenuity, prevents our applying the crucial test of the interference figures seen in convergent polarised light.

“Bertrand devised a form of microscope which enables these interference figures to be studied in the minute crystals seen in their rock sections, and von Lasaulx has improved this apparatus. We have what I believe to be the best form of the Bertrand-Lasaulx apparatus constructed by Nachet; but even employing an immersion objective magnifying 650 diameters, the crystals are still so small as to give neither rings, nor cross, nor brushes.

“I greatly regret that we have not been able to apply this test. I fear that no instrument exists which will accomplish what you desire; and Mr. Fletcher, on theoretical grounds, doubts whether it would be possible under any conditions to apply the test to such minute crystals.”

The largest crystals of squirrel's hæmoglobin that I have obtained were those formed by the addition of water to the defibrinated blood; they varied in size from  $\cdot 001$  to  $\cdot 005$  m. in breadth.

Since receiving Professor Judd's report, I have tried to obtain larger crystals by Gscheidlen's<sup>1</sup> method. He seals defibrinated blood in narrow glass tubes, which are then kept at a temperature of  $37^{\circ}$  C. for several days. On opening these tubes and emptying their contents into a watch glass, crystals of great size are formed from dog's blood after evaporation has occurred.

With squirrels' blood, however, I have not obtained larger crystals by this method than by the first. The reason for this seems to be the extreme readiness with which squirrels' hæmoglobin crystallises. It is a well-known fact that bodies that crystallise rapidly crystallise in small and numerous crystals. If some method could be devised for retarding, but not preventing, the crystallisation of squirrel's hæmoglobin, we might then be able to obtain crystals of it large enough to which to apply this crucial test.

<sup>1</sup> ‘*Physiologische Methodik*,’ p. 361.



The matter must therefore be left incomplete up to this point for the present. The probability, however, is greatly in favour of the crystals being true hexagons.

We have seen that in order to have a rhombic plate with hexagonal habit, it is necessary that one of its angles be approximately  $120^\circ$ . I measured the angles in the rhombic plates found in the rat, and found that they averaged  $129^\circ$ .

I shall also presently show that it is possible by the intermixture of the blood of different animals to obtain crystals closely resembling hexagons, but which are not so, as is shown by their optical properties.

*b. Mouse.*—Kunde was the first to describe the hæmoglobin crystals of this animal. He made eighteen observations, and the crystals he found were fine needles and prisms.

Bojanowski<sup>1</sup> was the next to make observations on these crystals. He describes and figures them as six-sided plates resembling in form those from squirrel's blood, of a flesh colour, and very soluble in water. He prepared them by the addition of a mixture of equal parts of alcohol and ether to the blood. No description of their optical properties is given. He remarks, "I have not been able to observe the fine needles described by Kunde."

Preyer repeated these experiments, and confirmed the observations of Kunde, not those of Bojanowski. He obtained small prismatic crystals.

I have myself experimented with the blood of eighteen mice, and the result has been again to confirm Kunde's observations. The crystals are exceedingly difficult to obtain, and in some cases I have had to repeat the process of freezing and thawing many times after the addition of alcohol, before succeeding in obtaining them. They are very soluble in water. The crystals are exceedingly small rhombic prisms. They are nearly colourless, and it is only when they are heaped together that any red tinge at all can be perceived in them. In one case in which by the addition of ether to the blood I obtained crystals of fair size after allowing the mixture to stand for five

<sup>1</sup> Bojanowski, 'Zeitsch. f. wiss. Zool.,' Bd. xii, 1863, p. 333.

days, the crystals still showed this same peculiarity, namely, in being nearly colourless. I have successfully employed Bojanowski's method for the preparation of the crystals, namely, the addition of a mixture of alcohol and ether to the blood; but in no case did hexagonal crystals form. Mouse's hæmoglobin also differs from squirrel's in being very soluble in water; this is admitted by Bojanowski; one would therefore expect a priori that its crystalline form would be different.

c. *Hamster (Cricetus vulgaris)*.—My remarks under this heading will be only historical. I have not myself been successful in obtaining one of these animals. The crystalline form of the hæmoglobin was first described by Lehmann, who found rhombohedra and six-sided plates. His experiments were repeated by Preyer,<sup>1</sup> whose observations on the subject are very complete. He found both crystalline forms, viz. six-sided plates, and rhombohedra. This is interesting since the rhombohedron belongs to the hexagonal system. By examination between crossed nicols he found that the six-sided plates had no action in "depolarising" the ray, and he therefore concludes that they, like squirrel's hæmoglobin crystals, are true hexagons.

d. *Conclusions*.—The presumption in favour of the hæmoglobin crystals of the squirrel and hamster being true hexagons is exceedingly great. In the case of the mouse, it seems to be almost equally certain that the crystals are not as a rule hexagonal. I should not like, however, to deny that hæmoglobin may sometimes in the case of the mouse crystallise in this way, because of some observations I have made on the hæmoglobin crystals of the rat.

Crystals are obtained from the blood of this animal with great ease; mere addition of water to the blood causes almost immediately an abundant crop of crystals. On this account the blood of this animal is used by the students in the practical classes at University College for the preparation of hæmoglobin crystals. Professor Schäfer told me that on looking over the students' preparations he had occasionally seen hexagons to-

<sup>1</sup> 'Die Blutkrystalle,' p. 262.

gether with the ordinary rhombic prisms and plates. In order to verify this, I have made numerous specimens of the crystals from the blood of about fifteen rats. As a rule, no hexagons were present; but on three occasions I have detected hexagonal plates—very few in number, perhaps not more than one or two on the slide—among the rhombic crystals. There appeared to be nothing special either about the animal used or the method employed in these cases. The diameter of these crystals averaged about the same as in squirrel's blood ( $\cdot 002$ — $\cdot 003$  m.). Between crossed nicols they also behaved the same as squirrels' hæmoglobin crystals, viz. remained dark in all positions.

In addition to this, if crystallisation be watched under the microscope, a single corpuscle will often be observed to set into a minute hexagon. This is what Preyer calls intraglobular crystallisation. He describes it as occurring in the blood of the hamster. It can also be observed in the blood of the rat. The crystals apparently so formed last but a few seconds, the corpuscles then becoming shrunken, or irregular, and very often under the subsequent action of water, globular. It is therefore possibly a stage in the crenation of the corpuscle. But, apart from this, it is undoubtedly the fact that hexagonal crystals are occasionally found in the blood of the rat.<sup>1</sup> It

<sup>1</sup> Since writing the above, I have received the following in a letter from Mr. Sheridan Lea, of Cambridge. He says :—"When I was showing a class how to put up permanent specimens of hæmoglobin crystals from rat's blood, we obtained uniformly hexagons, instead of prisms. This I have neither ever noticed or heard of before, and I thought it might be of interest to you. The method employed was that of Stein ('Centralb. f. d. med. Wiss.,' 1884, No. 23, and 'Virchow's Archiv,' 97, 483)." I had myself occasionally used Stein's method of preparing crystals from rat's blood, but had always obtained the usual rhombic prisms. On receiving Mr. Lea's letter I made a large number of preparations of hæmoglobin crystals by this method. The method consists in simply mounting a drop of defibrinated blood in a drop of Canada balsam. In the case of some animals, among which were man and the mouse, I was not able to get any crystals at all. In the commoner mammals, dog and cat, the crystals obtained were very fine specimens of rhombic prisms. In the guinea-pig and squirrel they presented the usual tetrahedral and hexagonal shapes respectively. With rat's blood, however, the results were

would therefore be possible that such crystals occasionally may occur in the blood of other animals, such as the mouse, the usual form of whose blood-crystals is, however, rhombic.

The rats employed in the above experiments were the common house rat, and also tame rats.

### 3. Influence of the other Constituents of the Blood on the Crystalline form of Hæmoglobin Crystals.

These experiments, as well as those in the next section of this paper, were undertaken at the suggestion of Professor Schäfer.

The blood-crystals of an animal have the same form whether they be obtained from the fresh blood, or from the blood from which the fibrin has been removed. Fibrin, or its precursor in the blood-plasma fibrinogen, has then no influence on the form of the blood-crystals.

The following experiments were undertaken to ascertain whether the other constituents of the blood-plasma, which are all contained in the serum, have any effect in influencing the form of the crystals.

The method of experimentation was as follows:—Defibrinated blood is taken in a tube and centrifugalised for about half an

very strange. In the majority of cases the usual rhombic needles were formed; but in a few cases I confirmed Mr. Lea's observations, and obtained perfectly regular hexagons; in some cases the hexagons would occupy one part of the slide only, while the remainder was filled with the ordinary prisms. Hexagons seemed to form where the proportion of blood to balsam was small, and they were formed especially at the edges of a preparation where the drop of blood had probably had time to dry somewhat before being covered with Canada balsam. These hexagons remained dark in the dark field of the polarising microscope. After a day or two they cracked in a peculiar way, and seemed then to be made up of minute needles radiating from a centre. This may or may not indicate the way in which they are formed. The fact that they occurred most in parts of the field where there was least water seems, however, to confirm the theory advanced later in the paper, viz. that the difference of crystalline forms in hæmoglobin is due to different amounts of water of crystallisation.



hour; the corpuscles settle at the bottom of the tube, and the supernatant serum is pipetted off. To the corpuscles the blood-serum of some other animal is added, the mixture shaken, and the mixture again centrifugalised; the serum is again pipetted off, and more added. After repeating this process several times, the corpuscles of one animal are obtained in the serum of another animal without any of the serum of the first animal being in the mixture. Hæmoglobin crystals are then prepared from this mixture. In some cases the foreign serum dissolves the hæmoglobin and disintegrates the corpuscles. This was first pointed out by Landois.<sup>1</sup>

Mere addition of the blood-serum of one animal does not as a rule cause the formation of blood-crystals. It does so, however, sometimes.<sup>2</sup> This is explicable on the assumption that the blood-serum used is very watery, and the hæmoglobin of the other animal crystallises very readily. I have myself come across no case in which it occurred.

My results may be best given in the form of the following table. I have given not only the effect of the foreign serum on the crystalline form of hæmoglobin, but also the effect on the corpuscles themselves, as to whether they are disintegrated or not.

Corpuscles of	In Serum of	Effect on the Corpuscles.	Effect on the Crystalline Form of the Hæmoglobin.
Rat	Squirrel	Much dissolved	Nil.
Squirrel	Rat	Very little dissolved	Nil.
Squirrel	Dog	Very little dissolved	Nil.
Rat	Guinea-pig	Little if any dissolved	Nil.
Guinea-pig	Cat	Nearly entirely dissolved	Nil.
Guinea-pig	Dog	Much dissolved	Nil.
Mouse	Cat	Little dissolved	Nil.

The result of these experiments is to show that the serum of one animal has no influence in causing a change of the hæmoglobin crystals of another animal.

I next examined in a qualitative manner the serum of certain

<sup>1</sup> 'Die Transfusion des Blutes,' Leipzig, 1874.

<sup>2</sup> An instance of such action is recorded by Professor Schäfer ('Blood Transfusion,' 'Trans. Obst. Soc. London,' 1879, p. 317).

rodents with regard to the proteids or albuminous substances contained in it. I obtained similar results in all animals, results which show, too, that the serum proteids of rodents agree with those in other mammalian animals which I had previously investigated.<sup>1</sup> The proteids, the most important bodies in the blood-plasma, being similar, the serum would not on a priori grounds be suspected of influencing the crystalline form of hæmoglobin. The results I have obtained with regard to the heat-coagulation temperatures of these bodies is shown in the following table.

Temperatures of Coagulation of the Proteids in the  
Blood of certain Rodents.

Name of Proteid.	Rat.	Water- Vole.	Mouse.	Guinea-pig.	Squirrel.	Rabbit
Globulins—	C.	C.	C.	C.	C.	C.
Fibrinogen . . .	56°	56°	56°	56°	56°	56°
Serum globulins .	75°	75°	75°	75°	75°	75°
Albumins—						
α . . . . .	73°	70°	70°-1°	72°	72°-3°	73°
β . . . . .	76°	77°	78°	77°	77° (small in amount)	77°
γ . . . . .	84°	84°	84°	87° (trace)	84° (very abundant)	84°

The stromata of the red blood-corpuscles might, however, possibly be supposed to have some influence on the crystalline form of the hæmoglobin. We have seen that crystallising the hæmoglobin of one animal from the serum of another yielded negative results; squirrel's hæmoglobin remained hexagonal, rat's and guinea-pig's rhombic prisms and tetrahedra respectively, whatever the serum in which they had been dissolved. A similar result followed crystallisation from a fluid consisting of serum plus the dissolved stromata of the corpuscles of some other animal. This was obtained by adding to the blood one sixteenth of its volume of ether, and letting it stand; the crystals of hæmoglobin which formed were filtered off, and the ether evaporated from the filtrate which consisted of the serum with the stromata of the corpuscles dissolved in it.

<sup>1</sup> Halliburton, "Periods of Serum," 'Journal of Physiology,' vol. v, p. 152.

So far then these experiments seem to show that the difference of crystalline form is due to some inherent quality of the hæmoglobin itself, and not due to any agency in the blood external to the hæmoglobin.

#### 4. The Crystalline forms of Hæmoglobin obtained by mixing the Blood from different Animals.

By mixing the defibrinated blood from two animals, whose hæmoglobin crystallises differently, and then preparing crystals, I thought I might obtain some new forms resulting from the mixture. Here my experiments have yielded mostly negative results, but the one positive result I have obtained from such experiments warrants me in recording the whole. The blood of two animals were mixed in about equal proportions, shaken thoroughly, and then hæmoglobin crystals prepared by the ether method.

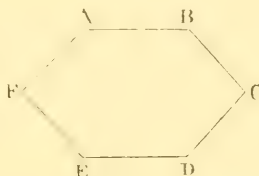
It will be convenient here again to give my results a tabular arrangement.

Blood of	Mixed with that of	Form of Hæmoglobin Crystals prepared from the Mixture.
Rat	Squirrel	Both rhombic prisms and hexagons present.
Rat	Guinea-pig	No rhombic prisms of the shape usually seen in rats' blood present. No tetrahedra. Crystals are all rhombic prisms with hexagonal habit.
Squirrel	Guinea-pig	Hexagonal plates and tetrahedra both present. Many tetrahedra imperfect. The tetrahedra were all reduced to about half the size of those prepared from the unmixed blood of the same guinea-pigs.
Dog	Squirrel	Fine rhombic needles and hexagonal plates both present in abundance.
Dog	Guinea-pig	The greater number of the crystals formed are very small tetrahedra, about a quarter the size of those prepared from the blood of the same guinea-pigs. The optical properties are, however, the same. Rhombic prisms very slender, like those of dog's blood, also seen.

The second case, that of mixing blood from the rat and guinea-pig, is interesting, and demands further description. It shows that it is possible to obtain a new form of hæmoglobin

by mixing that from two animals in which the crystalline form is different. It also shows that rhombic hæmoglobin crystals may assume a hexagonal type (fig. 4). These crystals are not, however, perfect or equilateral hexagons, two of the sides being longer than the other four.

FIG. 4.



The side  $AB = ED = \cdot 0019$  m. (average).

The sides  $BC = CD = EF = FA = \cdot 00125$  m. (average).

This irregularity is possibly to be accounted for by the fact that, in rats' hæmoglobin crystals, the angles corresponding to  $BCD$ ,  $A FE$ , are  $51^\circ$ . In order to obtain perfect hexagons of a rhombic type it is necessary, as before stated, that this angle be  $60^\circ$ .

Under crossed nicols these crystals appear perfectly bright, so contrasting with the true hexagons obtained from the blood of the squirrel and hamster.

This result was not, however, always obtained; in one or two cases I obtained as a result of mixing the blood of these two animals a mixture of crystals; that is prisms and tetrahedra.

##### 5. Can Squirrel's Hæmoglobin be obtained in any form other than Hexagonal Crystals?

Another set of experiments was performed with the object of breaking down the hexagonal constitution of the hæmoglobin of squirrels' blood. The first method tried was that of driving off the water of crystallisation, and of then adding water to the dehydrated hæmaglobin.

The hæmaglobin was obtained in a state of purity and dried over sulphuric acid until it lost no more weight. Then it was examined, and found to have its normal spectroscopic proper-



ties. It was heated to  $100^{\circ}$  C. in a water oven, and again examined. It had lost but a slight amount of weight. It was rather more insoluble in warm water than previously, but the spectroscopic properties, and the form of the crystals obtained from the solution, remained as before. This confirms the observation previously made by Hoppe-Seyler that dry hæmoglobin is not decomposed by a temperature of  $100^{\circ}$  C. It was again heated in the water oven at  $100^{\circ}$  C. until there was no further loss of weight. It was then heated to  $120^{\circ}$  C. in an air-bath, and again examined. It was found to have lost considerably in weight, to have lost its crystalline lustre, to be brown in colour (hæmatin) and to be insoluble in water. That is, it parts with its water of crystallisation at a temperature which decomposes it, with the formation of hæmatin, the proteid matter becoming at the same time coagulated and insoluble.

Experiments were then tried with the object of ascertaining whether a lower temperature will remove the water of crystallisation in a Torricellian vacuum. This I did by means of a Pflüger's mercurial air-pump. The action of the vacuum alone converted the dried hæmoglobin, at any rate partially, into the conditions of methæmoglobin. The water of crystallisation seemed to be completely lost at a temperature of  $50^{\circ}$ — $60^{\circ}$  C., as subsequent heating to  $120^{\circ}$  C. produced no further loss of weight. But this temperature was also sufficiently high to decompose the hæmoglobin in such a way as to render it insoluble, or almost so, in water, and therefore no crystals could be subsequently obtained from it.

The next method adopted was to convert the hæmoglobin by various reagents into methæmoglobin; then by reducing agents to form once more hæmoglobin, and then obtain crystals of this. But the reducing agents used were found to hinder the formation of crystals.

The third and simplest method was to repeatedly recrystallise the hæmoglobin, when it was found after three or four recrystallisations that no six-sided crystals were obtained, but a mixture of rhombic needles and tetrahedra, and in some cases the latter were absent. This is interesting in connection with

the reverse experiment already related, in which crystals simulating hexagons were obtained by mixing together the blood of the rat and guinea-pig, and in which the same result was obtained from a mixture of the solutions of the pure hæmoglobin of the same animals.

## 6. Conclusions and Remarks.

What the difference between the various forms of hæmoglobin may be, it cannot be a very deep or essential one. The difference in crystalline form is associated with a difference of solubility in water and other reagents; but the spectroscopic characters, the decomposition products, the compounds it forms, of which hæmin is a readily obtained example, are universally the same. Not only so, but Hoppe-Seyler has shown<sup>1</sup> that in various animals dried hæmoglobin has the same or nearly the same elementary composition.

Have we then to deal with a case of polymorphism? The terms dimorphism and polymorphism cannot be applied to any substance which crystallises in two or more forms, unless the composition of that substance be exactly the same in all cases. Instances of dimorphism in the mineral world are carbon and sulphur among the elements, and sal ammoniac, potassium iodide, cuprous oxide, &c., among compounds. The conditions on which dimorphism depend are two: first, temperature, secondly, the solvent from which the substance crystallises. If, as in the case of many mineral salts, the compounds are united with different proportions of water of crystallization, we have to deal with different hydrates, and the case is not one of true dimorphism; an instance of this is sulphate of soda.

The case seems to me to narrow itself down to this in the case of hæmoglobin; either we have here a case of polymorphism, or the crystalline forms are due to the combination with varying proportions of water of crystallisation. In the absence of a rational formula for hæmoglobin it would be unsafe to affirm the former of these two alternatives. Moreover, the conditions that are known to produce dimorphism in

<sup>1</sup> 'Physiologische Chemie,' p. 377.

minerals, namely, differences of temperature and of solvent, have in the case of hæmoglobin no influence.

If we then fall back on the latter alternative, the question which arises is whether there are any facts to support it. The explanation that the varying form of oxyhæmoglobin is due to varying quantities of water of crystallisation may be otherwise expressed by saying that we have to deal with different hydrates of oxyhæmoglobin. This would account for the varying solubilities of these substances in water and other reagents, and at the same time is not such an essential difference as to prevent the chief properties of hæmoglobin from being universally the same.

Turning to Hoppe-Seyler's researches on this subject of water of crystallisation, it is seen that its amount varies considerably. The following is his table:<sup>1</sup>

Percentage of Water of Crystallisation.					
Dog's hæmoglobin	.	.	.	.	3 to 4
Guinea-pig's „	.	.	.	.	7
Squirrel's „	.	.	.	.	9·4
Goose's „	.	.	.	.	9·4

In an earlier paper,<sup>2</sup> the same author gives rather different percentages, viz. for guinea-pig's hæmoglobin 6, for goose's hæmoglobin 7, and for squirrel's hæmoglobin 9. Dr. Christian Bohr<sup>3</sup> has more recently made observations on the water of crystallisation of dog's hæmoglobin, and as the result of thirteen experiments he finds that its amount varies from 6·3 to 1·2 per cent. It is thus seen that great variations occur in the numbers obtained by these experiments. The reason for this variation seems to me to be the great difficulty of obtaining hæmoglobin in a pure state, and also possibly because the method adopted, which is the same as that carried out in similar investigations on inorganic salts, is not applicable to such a complex and much less stable organic compound as

<sup>1</sup> 'Physiologische Chemie,' p. 377.

<sup>2</sup> 'Med. Chem. Untersuchungen,' Heft iii, 1868, p. 370.

<sup>3</sup> 'Experimentale Untersuchungen über die Sauerstoffaufnahme des Blutfarbstoffes,' Kopenhagen (Olsen and Co.), 1885.

hæmoglobin; in other words, the temperature necessary to drive off the water of crystallisation is also sufficient to cause certain decomposition changes in the pigment.

My experiments have shown that squirrel's hæmoglobin will under certain circumstances crystallise in forms other than the usual hexagonal form. A crucial experiment in order to see whether this is due to union with different amounts of water of crystallisation would have been first to ascertain the amount of this water in the hexagonal crystals, and then in the rhombic crystals obtained by recrystallisation. I have performed three such experiments, but the results obtained are so conflicting, and exhibit variations as great as in Bohr's experiments, that it is impossible to draw any conclusions from them, except the negative one that we cannot by our present methods of research make any definite statement with regard to the water of crystallisation of hæmoglobin.

Even if it be found ultimately that the difference in crystalline form is dependent on varying amounts of water of crystallisation, the difficulty is only explained up to a certain point. What is left unexplained is the nature of the agency that causes the hæmoglobin of some animals to unite with a certain amount of water of crystallisation, and that of other animals with a different amount. That some such substance or agency does exist would seem to be the inevitable result of the recrystallisation experiments which have been related.





## An Easy Method of obtaining Methæmoglobin Crystals for Microscopic Examination.

By

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METHÆMOGLOBIN is a derivative of the red colouring matter of the blood, concerning which a number of theories have been held. According to Sorby,<sup>1</sup> it is more highly oxygenated than oxyhæmoglobin; that is, it is a per-oxyhæmoglobin. Hoppe-Seyler,<sup>3</sup> on the other hand, regards it as a sub-oxyhæmoglobin, as it can be obtained under conditions which remove at least part of the oxygen of oxyhæmoglobin. According to both these views, however, the oxygen is regarded as being more firmly combined with the hæmoglobin than in the case of oxyhæmoglobin.

More recently, however, Hüfner and Külz<sup>3</sup> have advanced a third theory concerning the constitution of methæmoglobin, and that is that it contains the same amount of oxygen as oxyhæmoglobin, only in a closer state of combination. They are able to make this assertion from actual analyses; and these analyses were possible, inasmuch as they succeeded in obtaining methæmoglobin in a crystalline form. The method of obtaining these crystals is as follows:—Three or four cubic centimetres of a concentrated solution of ferri-

<sup>1</sup> 'Quart. Journ. Mier. Sci.,' 1870, p. 400.

<sup>2</sup> 'Zeit. Physiol. Chemie,' vol. ii, p. 150.

<sup>3</sup> 'Zeit. Physiol. Chemie,' vol. vii.

<sup>4</sup> G. Hüfner, "Ueber Krystallinisches Methämoglobin vom Hunde," 'Zeit. Physiol. Chem.,' Bd. viii, p. 366.

cyanide of potassium are added to a litre of concentrated solution of hæmoglobin. A quarter of a litre of alcohol is added, and the mixture frozen. After one or two days' exposure to this low temperature abundant crystals of a brown colour, which give the absorption spectrum of methæmoglobin, are deposited. They were obtained in this way from the hæmoglobin of the dog, pig, and horse, and their form is the same as that of the oxyhæmoglobin crystals of the same animals, i. e. rhombic prisms. Dr. Gamgee<sup>1</sup> had prepared these crystals from dog's blood many years previously, but their true nature was not at that time recognised. His method was much the same as Hüfner's, the chief difference being that the nitrite of potassium or amyl was employed instead of ferricyanide of potassium.

Jäderholm<sup>2</sup> has also obtained these crystals from dog's blood by the ferricyanide method, and confirms Hüfner's statement that they are rhombic prisms. He also figures some crystals of methæmoglobin obtained by Professor Hammarsten from the horse by the same method, which were regular six-sided plates, and showed no double refraction if lying flat; they therefore presumably belonged to the hexagonal system, and were more insoluble in water than the crystals of dogs' methæmoglobin. I can find no previous reference to the methæmoglobin crystals of rodent animals.

Hüfner's ferricyanide method is applicable when one wishes to obtain large quantities of the crystals for analysis. I now wish to describe a much simpler method of obtaining these crystals for purposes of microscopic observation. I have tried this method with the blood of the ox, dog, cat, rabbit, rat, guinea-pig, and squirrel, but only successfully in the three last-named animals. In other words, methæmoglobin crystals are obtained with ease from the same animals as yield oxyhæmoglobin crystals with readiness.

The method consists in taking a few cubic centimetres of

<sup>1</sup> A. Gamgee, "The Action of Nitrites on Blood," 'Philos. Trans.,' 1868, p. 589, et seq.

<sup>2</sup> 'Zeitschrift für Biologie,' Bd. xx, p. 419.

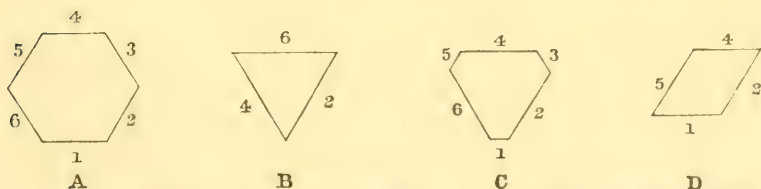
the defibrinated blood of the animal, adding an equal number of drops of nitrite of amyl in a test-tube, and shaking the mixture vigorously for a minute or two. The colour changes to the dark chocolate tint of methæmoglobin, and spectroscopic observation shows the typical absorption bands of that compound. A drop of this liquid is then placed<sup>1</sup> on a slide and covered; in a few minutes crystals form, which observation with the spectroscope shows to be composed of methæmoglobin. The edges of the cover-glass may then be sealed, and the crystals kept unchanged for several months.

The crystals obtained from guinea-pig's blood by this process are tetrahedra, which differ only in colour and spectroscopic appearances from those of oxyhæmoglobin from the same animal.

The crystals obtained from squirrel's blood are perfectly regular hexagonal plates, which remain dark between crossed nicols.

The crystals obtained from rat's blood are also perfectly regular hexagonal plates, which remain dark between crossed nicols, and which consequently are precisely similar to those of squirrel's methæmoglobin. This remarkable fact helps to show that the difference between the oxyhæmoglobin of these two animals cannot be a very deep or essential one.

In the case of rat's methæmoglobin there were, in addition to the hexagons, a few other plates of various shapes scattered



A. Regular hexagon. B. Equilateral triangle. C. Intermediate stage between A and B. D. Parallelogram.

<sup>1</sup> This must be done immediately after the formation of the chocolate-coloured liquid; as in about a quarter of an hour the whole liquid sets into a gelatinous mass of the same colour, from which no crystals are obtainable.



in different parts of the field. These are depicted in the accompanying cuts.

Mr. Fletcher kindly examined these for me, and expressed it as his opinion that the triangular and rhombic forms were merely variations of the hexagons. In the case of *B* faces 1, 3, and 5, and in the case of *D* faces 3 and 6 have virtually disappeared.

# On the Development of *Peripatus Novæ-Zealandiæ*.

By

**Lilian Sheldon,**

Bathurst Student, Newnham College, Cambridge.

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With Plates, XII, XIII, XIV, XV and XVI.

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THE account to be given in this paper is unfortunately by no means a complete one, owing to the difficulties attendant on working at the subject in this country. The great drawback is the difficulty of obtaining the creatures, and as, so far as I know, there is no way of keeping them alive in England, it is necessary to kill them and remove the embryos as soon as they arrive, so that one is by no means certain of obtaining the stages which are required, when one does have the good fortune to obtain a supply of the creatures.

All the embryos which I have worked upon were given to me by Mr. Sedgwick, and most of them were taken out of the uterus and preserved by him before he handed the material over to me. So far we are not able to state at what times of the year the different events in the development take place, but it is possible nevertheless that there may be a definite sequence, as we have at present only received the material in December, July, and April, and so have not many data to go upon.

The material which arrived in July contained seven females; three of these were without embryos in the oviduct or uterus, and the other four contained embryos varying in age from that

figured in figs. 25 and 26 to those which were just ready to be hatched.

The second supply arrived in November, but most of the creatures were not opened till December. One female, which was opened on November 27th, contained several fully developed embryos, while in one opened on November 30th the uterus was empty. Seven females which were opened in the middle of December contained only unsegmented and segmenting ova in their uteri.

In the last supply, which arrived last April, there were nine females, which were opened on the 18th day of the month. Of these five had no embryos in the uteri, one had several old embryos, one segmenting ovum, and two embryos, one of which is shown in sections in fig. 15; another contained several old embryos, one segmenting ovum (which is shown in section in fig. 11), and two of the stage represented in fig. 17; another contained the embryos, sections of which are shown in figs. 13, 18, 19, and 20, and also one unsegmented and several segmenting.

The New Zealand species, like all the others which are so far known, is viviparous, the embryos undergoing the whole course of their development in the uterus of the mother.

The ripe ovum is very large as compared with those of *Peripatus capensis* and *P. Edwardsii*, measuring about 1.5 mm. in its long axis. This large size is due to the enormous amount of food-yolk with which the egg is charged.

The egg is enclosed in a thick tough shell, which in the fresh state adheres closely to it; after treatment with certain reagents it becomes somewhat distended, and can be pricked or removed. This is especially the case with eggs which are preserved in hot corrosive sublimate, which causes the shell to swell up, to become less tough and to lie at a greater distance from the egg, so that it can be quite easily removed without damaging the surface of the egg. This is not so easily accomplished in cases where the corrosive sublimate was not heated, and the surface of several of my eggs was more or less injured in the process of removing the shell. It is necessary to prick

the egg-shell before placing the eggs in spirit, as otherwise it collapses and crushes the embryo. Before cutting sections of the eggs I almost always removed the shell, since it was too hard to cut well, and was also apt to prevent the paraffin from penetrating the ovum.

Within the shell the ovum is enclosed in a vitelline membrane, which adheres closely to it, and is thin and membranous. The two are easily distinguishable in eggs stained with picrocarmine, as the shell stains yellow and the vitelline membrane red.

The only accounts which have been hitherto published of the development of *P. novæ-zealandiæ* are by Hutton<sup>1</sup> and Kennel,<sup>2</sup> both of which are very brief. These observers state that the segmentation is holoblastic, which is not the case, it being rather on the centrolecithal than on any other type of segmentation.

#### METHODS.

The most satisfactory preparations obtained were from eggs which were preserved in hot or cold corrosive sublimate and glacial acetic acid mixed in the proportion of two to one. Other ova were preserved in Kleinenberg's picric acid, but these were not satisfactory. The eggs were all stained in picrocarmine, and afterwards passed through the various strengths of alcohol in which a small amount of picric acid was dissolved; by this method the yolk is stained yellow, the protoplasm light, and the nuclei deep red, so that they are easily distinguishable from one another. I am indebted to Mr. Harmer for the knowledge of this method.

The embryos were all removed from the uterus in the living state, and were preserved at once.

I do not purpose in this paper to enter into the subject of the ovarian ovum and the changes undergone by it in its

<sup>1</sup> Hutton, Capt. F. W., "On *Peripatus novæ-zealandiæ*," 'The Annals and Magazine of Natural History,' 4th Series, Nov., 1876.

<sup>2</sup> Kennel, Dr. T., "Entwicklungsgeschichte von *P. Edwardsii*, Blanch, und *P. torquatus*, n. sp.," 'Semper's Arbeiten,' Band vii, 1885.



passage into the ovum with the segmentation nucleus, as I hope to be able later to make some further investigations on that subject. It will be enough to state here that in several cases there were ova in the uterus which possessed no nucleus whatever; there was a small amount of protoplasm present as a very loose and not always easily-recognisable reticulum lying among the yolk-spheres. This protoplasmic reticulum was sometimes scattered throughout the egg, but was more often only present at the periphery; while in some cases it was aggregated at one point only. In one ovum there was a very large compact mass of protoplasm at one point near the periphery, but no trace of a nucleus could be discerned.

#### SEGMENTATION.

Immediately before the segmentation begins the ovum consists of a great mass of yolk-spheres, and contains a single nucleus. The position of the nucleus in the ovum varies somewhat in different cases; in fig. 1 it is seen to be situated at some distance from the periphery of the ovum; in this case it is round in form, and contains a deeply staining wall and also a single mass of chromatin. The protoplasm in which it is embedded is compact and dense, and contains at its periphery several chromatin particles. In the ovum from which fig. 2 is taken the nucleus and its surrounding protoplasm had a somewhat different position and form. The nucleus is situated near the periphery of the ovum, being separated from the vitelline membrane by only a thin layer of yolk. The nucleus has a peculiar lobed form, and consists of three masses of deeply staining material, between which is a portion of nuclear substance which stains less deeply. It is surrounded by a very small amount of protoplasm, which forms a loose reticulum, the strands of which pass in and are lost among the yolk-spheres.

The next stage is that in which two nuclei are present in the egg; two sections from such an egg are figured in figs. 3 *a* and 3 *b*. One nucleus is situated at the periphery of the ovum and the other somewhat deeper, but both lie in the centre

of one of the long surfaces on the same side of the ovum, and each is surrounded by a protoplasmic area. The peripherally-situated nucleus had a peculiar lobed form, while the other seemed to be in the act of dividing, the chromatic particles representing the spindle-fibres cut through transversely. In another ovum, in which two nuclei were present, both were situated quite near the periphery; but in this case the sections were too thick for the structure of the nuclei to be made out.

In the next stage, in which three nuclei are present, other changes have also taken place in the ovum. These concern the segmentation of the yolk. At the pole where the nuclei are situated the yolk is broken up into segments, which vary considerably in shape and size. The yolk-spheres at this pole are smaller than those over the rest of the egg. The yolk segmentation does not bear any definite relation to the protoplasmic and nuclear segmentation, but takes place quite independently of it. A nucleus is present in each of three of the yolk-segments, in others there is a considerable protoplasmic reticulum, but no nucleus, while in others again there is no trace of either protoplasm or nucleus. The nuclei are all situated near together. Fig. 4*a* is a section through the whole egg. The section passes through one nucleus which is round in form and contains a chromatin network, and is surrounded by an area of protoplasm. It is situated in a yolk-segment, the spheres composing which are very small. The section passes through several other yolk-segments, four of which contain no recognisable protoplasm or nucleus; another, which is not completely segmented off from the mass of the yolk, contains a small compact mass of protoplasm. The greater part of the yolk is unsegmented, and is composed of very large yolk-spheres. In future that part of the surface of the ovum at which the nuclei are situated will be spoken of as the protoplasmic area. Figs. 4*b* and 4*c* are taken from other sections through the same egg, and represent sections of the protoplasmic area seen under higher power. In fig. 4*b* there is a considerable amount of protoplasm in two of the yolk-segments besides that in which the nucleus is present. The nucleus is

embedded in a large mass of protoplasm, and is very much lobed in form. In fig. 4 *c*, which passes through the third nucleus, two of the yolk-segments possess a small amount of protoplasm, and there is a very large amount in the segment which contains the nucleus. The nucleus itself is very peculiar in shape, and is made up of a large number of lobes.

At the next stage the yolk is segmented throughout the whole egg, but the nuclei are still confined to the protoplasmic area. In the fresh state the yolk-segments are very clearly seen over the whole surface, so that in a view of the whole egg it appears to be made up of a number of round segments, all resembling one another in size and shape; a surface view of such an egg is figured in fig. 23. It is this appearance which probably led Hutton and Kennel to state that the segmentation was holoblastic, but the fact that it is only due to the yolk segmentation is quite clear when sections of the egg are examined.

The yolk-segments are much smaller at the protoplasmic area, and the yolk-spheres composing them are also smaller than they are over the rest of the egg.

The protoplasm is still mainly confined to the protoplasmic area, but small quantities are present in other regions; it consists of a reticulum very indefinitely segmented, the whole being intimately connected by strands passing over from one aggregation of protoplasm to another. Nuclei are scattered about very irregularly through the protoplasm, in some places two or three lying close together, while in others there is a considerable tract of protoplasm devoid of any nucleus. Sections through the protoplasmic area of such an egg are shown in figs. 7 *a* and 7 *b*.

A surface view of an egg slightly older than the preceding is shown in fig. 24; the yolk segmentation on the surface of the egg has been obliterated in the course of preservation, but at the protoplasmic area the segments are clearly seen, the presence of the protoplasm having rendered the surface at this point less easily disintegrated. This egg bears a very close resemblance to those figured by Mr. Sedgwick in the first part

of his work on the 'Development of *P. capensis*' (fig. 7). A section through the protoplasmic area of this egg is shown in fig. 5. The protoplasmic masses, which in surface view appeared to be separate from one another, are seen to be very closely connected by strands; in two places two nuclei are seen lying close to one another, and in another a single nucleus is cut through. The yolk, situated below the protoplasm, is segmented. Fig. 6 represents a section of a small portion of the protoplasmic area drawn under higher power, in which a large number of nuclei are crowded close together in a small area of reticulated protoplasm.

In the next stage the protoplasmic segments with their nuclei extend over a somewhat larger area of the surface of the egg, the nuclei being still very irregularly scattered through the protoplasm. This extension of the protoplasm is shown in fig. 8, which is drawn from the protoplasmic area of a section of this age. The segments are rather more distinct from one another than they are in the eggs so far described, but they are still connected by protoplasmic strands. The yolk is very definitely segmented. Fig. 9 is from a section through an egg of about the same age; in it the protoplasmic segments are much more distinct than is usually the case at this stage.

In all the above-described stages many of the nuclei show indications of karyokinetic figures, so that it is probable that all the nuclei are derived by division of the first segmentation nucleus, and it is not necessary to suppose that any process of free-nuclear formation has taken place.

In the latest segmentation stage which my material has provided the protoplasmic segments extend over rather more than half the surface of the ovum. They are arranged in a regular layer near the periphery, and appear to be more definitely separated from one another than in the previous stages, although it is probable that they are connected by strands which are hidden by the yolk which separates them. Nuclei are present in many of the segments, although some are devoid of them. In the centre of the protoplasmic area



there is a mass of protoplasm lying quite on the periphery, and extending over it for a small area. In it there is a large round nucleus with very evident traces of a karyokinetic figure. Small irregular branched masses of protoplasm are present near the periphery at the lower side of the egg, but they contain no nuclei. In the centre of the egg there are two or three very definite protoplasmic masses, none of these contain nuclei, but in one there are three very definite chromatin granules. Fig. 10 represents a section through this ovum.

Between the last-described ovum and the next one which I have, there is a considerable gap. In this ovum, a section through which is represented in fig. 11, the yolk is still segmented, and nuclei are present scattered irregularly throughout the ovum, being more plentiful near the periphery than towards the centre. In one region there is a special aggregation of nuclei lying in a loose protoplasmic reticulum; this mass of nuclei is situated on one surface of the egg, its long axis being parallel to the long axis of the latter, and extending through about the middle third of its length. In transverse section it is irregularly triangular in shape, the apex being directed towards the centre, and the base forming the periphery of the egg in this region. The protoplasmic reticulum passes without any sharp line of demarcation at its edges into the yolk. Fig. 12 represents the protoplasmic portion of the ovum; it is drawn from the same section as fig. 11, but under Zeiss' obj. D instead of obj. A. The nuclei vary much in size, and some stain very much more deeply than others; they are extremely irregularly arranged, there being in some places a group of several crowded close together in a small area of protoplasm; this is very noticeable in one place in fig. 12, where eleven small nuclei lie together in a small oval mass of protoplasm; in other places they are much farther apart, and sometimes there is a fairly large area of protoplasm devoid of nuclei. A few yolk-spheres are present among the meshes of the reticulum. There is no trace of any cell boundaries, the protoplasm forming a very loose reticulum, the whole mass being everywhere connected together by strands. The impos-

sibility of fixing cell limits is rendered still more obvious by the irregular arrangement of the nuclei. Traces of a chromatin network, more or less distinct, are visible in most of the nuclei; the smaller ones as a rule stain more deeply than the larger.

A section of an ovum of the next stage is figured in fig. 13, in it the reticulum of the protoplasmic area has become much more compact, and is flattened against the surface of the egg. At the same time its width laterally has increased, so that it spreads over a larger surface at the periphery of the egg. In fact the protoplasmic area might be described as forming a flattened plate on one surface of the ovum, throughout rather more than one third of its length; the lateral edges of the plate show a slight tendency to turn inwards away from the periphery of the egg. A trace of the triangular shape presented by the protoplasmic area in the last stage still persists in a low pointed ridge which runs along the middle of the plate, and projects inwards towards the centre of the ovum. Fig. 14 represents the protoplasmic area, it is drawn from the same section as fig. 13, but under a higher degree of magnification. In it the protoplasm is seen to consist of a fairly close reticulum, in which the nuclei are packed very near together. The nuclei themselves possess the same characters as those shown in fig. 12, and like them are of various sizes. There is still no trace whatever of any cell divisions, the protoplasm forming a continuous mass in which the nuclei lie quite irregularly. The tendency of the lateral edges of the plate to turn inwards is shown in this figure. Nuclei are still present scattered through the yolky part of the ovum, and, as in the last stage, are more numerous towards the periphery. Traces are visible of the segmented character of the yolk, but this is not very clearly shown owing to the yolky part of the egg having broken and fallen out to some extent in the course of cutting the sections.

Between this stage and the one now to be described there is again a large gap. A transverse section through the middle region of the egg is shown in fig. 15 c; in it the appearance is

as follows:—The egg is bounded externally by the vitelline membrane (*v. m.*); beneath this and closely applied to it is a peripheral layer of yolk (*p. y.*), in which are present a number of small round, highly refractive bodies, which stain very deep red with picocarmine. Within this peripheral yolk layer and forming a ring round the egg is a thin layer of protoplasm (*Ec.*), with clearly defined inner and outer boundaries, and a single layer of nuclei arranged regularly in it. At one point there is a great proliferation of nuclei forming a conspicuous mass (*p. n.*) on the outer side of the protoplasmic ring; its boundaries are not very sharply defined, so that it passes at its edge into the yolk without any clear line of demarcation separating the two. The space inside the ring of protoplasm is filled with yolk.

In passing through the series of sections from the middle one just described towards one end of the egg, the proliferating mass of nuclei is found to gradually thin out, and finally disappear, so that, as is shown in fig. 15 *d*, the protoplasmic band (*Ec.*) comes to be of the same thickness along its whole circumference. At the same time the diameter of the ring gradually diminishes, and it finally ends not far from the extremity of the egg as a cul-de-sac, the blind end of which is enveloped in the peripheral yolk.

Passing from the central section towards the other end of the egg, the proliferating mass of nuclei increases in size, and then becomes divided into two masses (vide fig. 15 *b*, *p. n.*). These masses are not completely separated from one another, but are connected above and below by a layer of protoplasm, in which nuclei are present, so that a second cavity is produced (fig. 15 *b*, *p.*) lying below that enclosed by the protoplasmic ring, and bounded laterally by the proliferating mass of nuclei, and above (*Sep.*) and below by the bands of protoplasm which connect these together. Near the extremity of the egg both these cavities end blindly, the secondary one, i.e. that which lies between the proliferating masses, ending a little before the original cavity. The blind end of the latter is enclosed in the peripheral yolk, which at this end of the eggs shows signs of

the original yolk segmentation, and contains a good many nuclei (fig. 15 *a*).

Cell outlines are not distinct at this stage, but indications of them are present between the nuclei of the protoplasm bounding the sac. There are no traces of any cell boundaries in the proliferating mass of nuclei.

The structure of the egg at this stage may be briefly described as follows:—The egg is surrounded by a vitelline membrane; beneath this is a peripheral layer of yolk containing small round, highly refractive bodies; within this is a sac ending blindly at both ends, bounded by a layer of protoplasm, which is one cell thick, except along one line, where, throughout most of its length, there is a longitudinal ridge composed of a mass of proliferating nuclei, among which many of the small round, highly refracting bodies are scattered. At one end this ridge thins out and gradually disappears; towards the other it increases in thickness, and by the parting of its lateral walls comes to enclose a secondary cavity, which lies below the primary sac, and ends blindly shortly before the latter. The sac is filled with food yolk, in which a few scattered nuclei are present.

By a comparison of this embryo with those of later stages it is found that the internal sac, together with the proliferating ridge, represents the embryonic part of the ovum, the single layer of protoplasm being the ectoderm of the embryo. The mesoderm and ectoderm are not yet definitely differentiated. The peripheral yolk does not form any part of the future embryo, but seems to be absorbed as food material.

The most tenable hypothesis, whereby this stage can be connected with the previous one, is that the cells at the edges of the protoplasmic plate of the latter grow round the ovum in a normal epibolic manner, except that, instead of spreading over its surface, they grow round slightly internal to it, so as to leave a peripheral layer of yolk outside them. A small quantity of this peripheral yolk inserts itself between the protoplasmic plate and the vitelline membrane, so that the whole embryo is surrounded by yolk. The protoplasmic plate itself probably



forms the proliferating ridge. The small round, deeply staining bodies found in the peripheral yolk have no obvious rudiment in the previous stage; they present no definite structure, and, except for their property of staining deep red with picrocarmine, they resemble the yolk-spheres. It is possible that they may be derived by the breaking down and alteration of the nuclei which were present in the yolk in the previous stage. This view as to their origin is supported by the fact that they are very much more numerous in the peripheral than in the central yolk, which was also the case with the nuclei. Whatever their origin may be, they probably function as food material, as to a certain extent at this stage, and very largely in later ones, they are found lying among the cells of the embryo.

By the next stage again the ovum has undergone considerable changes; the peripheral yolk is mostly absorbed, but the small round bodies are still very numerous, lying both outside the embryo, i. e. between it and the vitelline membrane, and also among the cells of the embryo, thereby rendering the exact boundaries of the latter difficult to distinguish. In a transverse section through the egg, near its anterior end, the embryo is seen as a sac surrounded by a layer of ectoderm, which is rendered somewhat indefinite by the intrusion of the small round bodies. At the ventro-lateral corners there is a pair of proliferating masses of nuclei, which are the rudiments of the præoral lobes. As in the last stage, the whole embryo is filled with yolk. A section slightly posterior to this is shown in fig. 17 *a*; in it the rudimentary præoral lobes (*p. o. l.*) are present, though they are rather smaller than they were in the section last described; lying between them, on the ventral face of the embryo, is the transverse section of the tip of a small second sac (*post. Em.*), which is bounded by a fairly definite layer of nuclei, and contains in its interior yolk-spheres, small round bodies, and a few large nuclei. In a section through the middle region of the ovum, such as is figured in fig. 17 *b*, the second sac is found to have increased in diameter, and to lie on the ventral face of the primary sac, from which it is separated by a protoplasmic septum. Proliferating masses of

nuclei (*Mes.*) are present at the ventro-lateral corners of the primary sac, and there are also indications of a proliferation of the nuclei at those corners of the secondary sac which are apposed to the thickenings on the primary one.

In a section through the posterior region of the egg (such as is represented in fig. 17 *c*), the septum dividing the two sacs from one another has disappeared, so that they are in free communication with each other. Thus the central cavity of the embryo is continuous from the anterior extremity of the embryo round the posterior end of the egg to the tip, which was found lying on the ventral face of the head of the embryo between the præoral lobes (vide fig. 17 *a*, *post. Em.*) The longitudinal thickenings along the ventro-lateral borders of the sacs coalesce shortly behind the point where the septum disappears; that is, the thickening on the right of the primary sac coalesces with that on the right of the secondary one, and similarly those on the left; so that on each side of the embryo there is a thickened ridge which starts just behind the præoral lobes, and is continued round behind the septum along the sides of the ventral sac. These thickenings are the mesoderm. The endoderm is only represented by a few scattered cells in the yolk which fills the embryo. The embryo, therefore, consists of a sac which, except at the posterior end of the egg, is divided into a dorsally- and a ventrally-lying one by a longitudinal horizontal septum. The whole embryo is filled with yolk, and is surrounded by a thick layer of the small round bodies, outside which is the vitelline membrane.

Several intermediate stages are obviously wanting between this embryo and the previous one, and it is therefore not possible to state positively how the one develops into the other. It seems possible, however, that the cavity (figs. 15 *b*, *p*) which was present in the proliferating mass of nuclei in the previous stage, corresponds to that which constitutes the ventral sac in the anterior portion of the egg last described (fig. 17 *a*, *post. Em.*). If the proliferating mass were anteriorly to divide completely, only remaining attached by a string of cells on the ventral surface of the embryo, constituting the ventral ectoderm,

a condition would be attained similar to that found at the extreme anterior end of the embryo, the now paired proliferating masses being the præoral lobes. Farther back the condition would be similar to that found in fig. 15 *b*, in which the proliferating mass has divided centrally, but the divided masses remain connected above and below by a string of cells, so as to enclose a secondary cavity lying on the ventral face of the primary one, the two being separated only by a thin layer of protoplasm. This may be seen by comparing fig. 15 *b* with fig. 17 *b*; in the latter section the proliferating mass on each side has divided, part being applied to the ventro-lateral corner of the ventral and part to the apposed corner of the dorsal sac (fig. 17 *b*, *Mes.*). The condition found in the posterior region of the last-described embryo (fig. 17 *c*) would be attained if the proliferating mass divided, only remaining connected by a layer of cells above, so that no septum would be present dividing the cavity of the embryo into two.

The main difference between this stage and the next may be best seen on examination of a section through the middle region of the ovum. In such a section (fig. 18 *b*) the two cavities, which were before only separated from one another by a single layer of protoplasm, are entirely distinct; each being bounded on all sides by a definite protoplasmic layer, and the walls, which are apposed to one another, being completely separated by a narrow space in which are found some of the small round elements, which are present in the space between the embryo and the vitelline membrane. Posteriorly the two sacs communicate as before (fig. 18 *c*); anteriorly the præoral lobes are very prominent (fig. 18 *a*, *p. o. l.*), there is a slight invagination of ectoderm (*St.*) in the middle ventral line, where the mouth will be found later, and there is a pair of definite hollow somites, which are the somites of the præoral lobes, lying one on each side of the yolk (fig. 18 *a*, *S. 1.*). The proliferations of nuclei which constitute the mesoblast are much larger and more clearly defined than in the last stage (*Mes.*) The peripheral yolk is entirely absorbed, but the whole embryo is still surrounded by the small round

elements, which are also very plentiful lying among the cells of the embryo, especially in the præoral lobes, and in the somites. These bodies, which are represented drawn under a high power in fig. 16, have a somewhat different form in this egg to that which they have in the previously described ones; they are still round in shape, but they contain in their interior a larger or smaller amount of vacuoles. The region in which the embryo is doubled on itself is shorter in this egg than in the preceding stage.

As was mentioned before the main difference between this and the previously described embryo is in the complete separation of the two sacs in that region where they are superposed upon one another. This change seems to have been effected by the ingrowth of the surrounding tissue, which by pushing in the septum causes it to become double. This process had already begun in the anterior region of the ovum of the previous stage, where in fig. 17 *a* the ventral sac is seen to be surrounded by a complete layer of ectoderm, while more posteriorly in the egg it is only separated from the dorsal sac by a single septum, as is shown in fig. 17 *b*.

In the next stage, sections of which are figured in figs. 19 *a—d*, the separation between the cavities has progressed still farther, the anterior tip of the ventral cavity, i. e. the posterior tip of the embryo, lying at some distance from the ventral wall of the dorsal one, as is shown in fig. 19 *b*. The region in which the embryo is doubled on itself is also shorter than before, so that it seems to be gradually straightening itself out. The embryo has also advanced considerably in other respects—the mouth is present as an ectodermic invagination (fig. 19 *b*, *M.*), the inner end of which forms the pharynx; the præoral lobes are united in front of the mouth by the cerebral commissure (fig. 19 *a*, *Cer. Com.*); the somites are present as a series of paired, hollow, thin-walled vesicles lying on the lateral faces of the body below the ectoderm, which in this region is slightly thickened. In the posterior portion of the body the somites are not yet present (fig. 19 *c*, *Mes.*), the mesoblast being still in the form of a pair of proliferating ridges of cells. The endoderm



is now for the first time clearly differentiated, and consists of a layer of nuclei surrounded by a very loosely reticulate layer of protoplasm, around the periphery of the inner yolk mass, and just within the ectoderm, except in the region of the somites, where it is subjacent to the splanchnic wall of the latter (figs. 19 *a—d*, *End.*). The small round bodies are still present, but in much smaller quantities than hitherto, both outside and among the cells of the embryo, from which fact it may be inferred that most of them have been absorbed; this reduction is shown in all the four figures (19 *a—d*).

In the next stage the straightening of the embryo within the shell had considerably progressed, the posterior end only being bent at an angle to the main part of the body. There is as yet no anus, so that the stomodæum is formed considerably earlier than the proctodæum. The somites are very distinct, with a thin splanchnic (fig. 20, *sp.*) and a thick somatic wall (fig. 20, *so*); they do not contain in their cavities any of the small round elements found in them in previous stages. The ectoderm of the lateral body wall, i.e. that covering the somites, is thickened, and in the ventral regions of the thickening rounded elements are present, which will give rise to the future nerve-cords (fig. 20, *n. s.*). In the central yolk of this embryo (fig. 20) there are traces of the yolk segmentation, some of the segments containing nuclei; whether these traces have really been retained in this particular embryo longer than usual, or whether in the last few eggs which have been described they have been destroyed by the action of reagents is doubtful; the latter interpretation, however, seems possible, since in young segmenting embryos whose yolk could in the fresh state be very clearly seen to be segmented, the segmentation was only partially discernible in sections of them when preserved.

In all the eggs of stages subsequent to the segmentation which have been described hitherto, it was not possible to make out anything in a surface view of the embryo either in the fresh state or after preservation, owing to the peripheral yolk which surrounded it and completely obscured its external

characters. But in the next stage the peripheral layer has all become absorbed, and after the removal of the shell the features of the embryo can be clearly made out. Figs. 25 and 26, which represent an embryo of this stage seen from the side and front respectively, were drawn from an embryo after it had been preserved. The præoral lobes are very prominent, and are separated from one another ventrally by a rather shallow, wide median groove; the antennæ are beginning to bud out as small protuberances on their anterior dorsal corners. Along each side of the body is a longitudinal ridge, which is very clearly discernible by its prominence and also by its opaque white colour. This ridge is the origin of the appendages, and is anteriorly divided into distinct lobes, which are the rudiments of the appendages of the anterior segments of the body. The posterior end of the embryo is bent up almost at a right angle to the rest of the body, and at the tip where the lateral ridges meet there is a small papilla, which is perforated by the anus. The mouth is visible, situated on the ventral surface immediately behind the præoral lobes. Except on the præoral lobes, the lateral ridges, and the anal papilla, the body of the embryo is a dull yellowish colour, which is due to the yolk shining through the thin ectoderm.

In a series of transverse sections (figs. 21 *a*—*c*) through this embryo the following points are noticeable:

The ectoderm, except over the præoral lobes and the appendicular ridges, is a thin layer of flat cells. The cerebral lobes of the nervous system (fig. 21 *a*, *br.*) are connected in front of the mouth by a transverse commissure (fig. 21 *a*, *Cer. Com.*). The ventral cords are continuous with the brain, and form a pair of longitudinal ectodermic thickenings on the inner ventral angles of the leg ridges (figs. 21 *b* and 21 *c*, *n. s.*); they are not definitely separated from the ectoderm, but are distinguishable from it by the round elements of which they are composed. The mouth opens into a thick walled pharynx (fig. 21 *a*, *Ph.*), which is in communication with the gut. The anus is present (fig. 21 *c*, *an.*) on a terminal papilla, and is formed by a simple invagination of ectoderm. Immediately

behind the anus in the middle line there is a mass of undifferentiated cells (fig. 22, *pr. st.*), which is the primitive streak, a groove running down its centre being the primitive groove (fig. 22, *pr. gr.*). This is the earliest stage at which these structures are present, and the cells do not appear to be in a state of great activity.

The Mesoderm.—The somites are present as a series of paired hollow cavities on each side of the embryo. Their inner or splanchnic walls are very thin (figs. 21 *b* and 21 *c*, *Sp.*), but their outer are much thickened, and are composed of several layers of nuclei (figs. 21 *b* and 21 *c*, *So.*). In the anterior somites (fig. 21 *b*) the somatic wall has pushed out the thickened overlying ectoderm so as to form protuberances, which are the rudiments of the legs. A slight ventral outgrowth of the somatic wall towards the ectoderm is the rudiment of the duct of the segmental organ (fig. 21 *b*, *n. d.*). The posterior pair of somites communicate with one another across the middle line, and their posterior walls are fused with the undifferentiated tissues of the primitive streak.

The endoderm is present in the form of a layer of fairly regularly arranged nuclei lying in a protoplasmic reticulum round the periphery of the yolk (figs. 21 *a—c*, *End.*). There are a few nuclei in the central yolk, which latter is much less voluminous than in previous stages.

#### GENERAL CONSIDERATIONS.

The Segmentation.—So far as my material has allowed me to investigate the subject, the segmentation of *Peripatus novæ-zealandiæ* resembles closely that which has been described in some other Arthropoda. Quite lately Henking,<sup>1</sup> among others, has described the segmentation in the eggs of certain Phalangidæ, and his account in many respects agrees with that which I have given, noticeably in the formation of the blastoderm and in the irregular arrangement in the young stages of the nuclei composing it. The segmentation of the

<sup>1</sup> Henking, H., "Untersuchungen über die Entwicklung der Phalangiden," Theil i, 'Zeit. für wissen. Zool.,' xlv, 1886.

yolk, however, differs in that he considers each yolk-segment as a single cell, whereas in *P. novæ-zealandiæ* I find no relation existing between the yolk and the nuclei, it being quite a matter of chance whether or not a yolk-segment possesses a nucleus. Moreover, I do not think it necessary to suppose any free nuclear or cell formation to exist in the formation of the blastoderm, as there seems to be no reason why all the nuclei forming it should not be derived by division of the original segmentation nucleus. As to the nuclei which appear in the central part of the yolk, it is more difficult to account for them as originating from any pre-existing nucleus, as they are very far removed from any one, and the three chromatin particles in a mass of protoplasm, which are figured in fig. 10, rather point to the formation of nuclei by a process of aggregation of such particles. The segmentation also bears a considerable resemblance to that of *Peripatus capensis*; in fact the differences between the two may in all probability be accounted for by the presence of the yolk in the New Zealand species. They also resemble one another in the absence of any cell outlines, the protoplasm in *P. novæ-zealandiæ*, as in *P. capensis*, forming a perfectly continuous reticulum in which the nuclei are embedded; this is very especially noticeable in certain stages in the former species, as is shown in fig. 12. The curious forms assumed by the nuclei also resemble those found in *P. capensis*, although owing to the difficulty presented by the yolk in cutting sections of the young stages I was not able to get sections sufficiently thin to enable me to examine them in detail. It is nevertheless perfectly obvious that the nuclei often present the same curious phenomenon of being divided by septa into numerous compartments. These two points, however, viz. the continuity of the protoplasm and the forms of the nucleus, have been sufficiently discussed by Mr. Sedgwick in his papers on *P. capensis*, and need not be further considered here.

The mode of development from the segmentation up to the two last stages described in this paper presents many very curious facts, and indeed, so far as I know, is without any



exact parallel in the animal kingdom. It is particularly unfortunate that so many stages are wanting in my material, so that the exact sequence of events cannot be stated with any certainty. It seems strange that the early stages of all the three species of *Peripatus* should differ so remarkably from one another, while the later course of development seems to be nearly similar in all three.

It might be said of the mode of development of *P. novæ-zealandiæ* that the embryo is formed by a process of crystallising out in situ from a mass of yolk among which is a protoplasmic reticulum containing nuclei.

The two most remarkable features in the development are perhaps the mode of nutrition of the embryo and the mode of formation of the posterior part of the embryo, and it will be more convenient to discuss these two separately.

Mode of Nutrition of the Embryo.—As has been shown the embryo derives nutriment from two sources, (a) the yolk contained within its body; (b) a peripheral layer of yolk in which are embedded numerous small round, highly refractive bodies. The former of these sources need not be considered, as it is similar to that which occurs in many other eggs, which are loaded with food-yolk, being present in the hypoblast, but entirely absent in the mesoblast. It is with the peripheral yolk that we are concerned. The complete envelopment of the ovum in a thick peripheral layer of yolk is a very remarkable and unusual mode of embryonic nutrition, but its object evidently is to supply the ectoderm with a constant source of nourishment, the yolk first and the small round bodies eventually being completely absorbed by the ectoderm cells. It seems possible to regard it as ectodermal yolk, and it is very probably homologous with the peculiar arrangement in the ectoderm cells of *Peripatus capensis* which Mr. Sedgwick has described in the region of the hump. He says (Part III, p. 472, 'Quart. Journ. Mic. Sci.,' vol. xxvii): "This increase in thickness" (i. e. of the ectoderm) "is mainly due to the appearance, outside the nuclei, of a layer of vacuolated protoplasm. The vacuolation . . . . is a

very striking feature. The surface of the dorsal ectoderm, particularly of the hump, is very rough in these stages, and in the best preserved embryos without a definite external boundary. It presents very much the appearance which a bath-sponge would present in section, fraying out, as it were, into the surrounding fluid; and one may fairly conclude that during life it possesses the power of sending out processes into the fluid surrounding the embryo, and that the superficial vacuoles open to the exterior. In short, I am inclined to think that this surface ectoderm during stages E to F has a nutritive function, absorbing the fluid in which the embryo lies, and it seems to me conceivable that the placenta described by Kennel in the Trinidad species may be a more specialised organ of the same nature." It seems also conceivable that the peripheral layer of yolk in *P. novæ-zealandiæ* may be a more specialised organ of the same nature, and that originally when the ovum of *P. capensis* was provided with yolk, the space between the egg membrane and the ectoderm was filled with yolk, as is the case in *P. novæ-zealandiæ*, instead of as now with fluid. I have not been able to find processes on the external surface of the ectoderm cells, but the boundary is not very sharp, and the protoplasm passes without any definite limits into the peripheral layer. This is specially the case in the stages in which the internal yolk is divided by a longitudinal horizontal septum (vide fig. 17 *b* and 17 *c*). The modes of nutrition of Arthropod embryos are, as is well known, very variable, and an arrangement somewhat comparable to this is described by Ganin<sup>1</sup> as existing in *Platygaster*, where a layer of protoplasm containing nuclei surrounds the embryo, both the protoplasmic layer and the embryo being derived from precisely similar elements. He describes the first nucleus as arising as a new formation in the egg; from this another nucleus arises by division, and from this second one a third. The original nucleus gives rise by a process of complete segmentation to the embryo, two later ones undergo division, and becoming sur-

<sup>1</sup> Ganin, M., "Beiträge zur Erkenntniss der Entwicklungsgeschichte bei den Insecten," 'Zeit. für wiss. Zool.,' xix, 1869.

rounded with protoplasm, arrange themselves as a layer round the embryo, in the formation of which they play no part. He does not say that this layer is used as food material, but considers it as a protective layer comparable in physiological significance to the amnion of an ordinary insect development. This process is very similar to that which occurs in *P. novæ-zealandiæ*, with the exception that the yolk is entirely wanting in the eggs of *Platygaster*. The peripheral yolk layer probably serves both as a nutritive and a protective layer, acting as a shield for the embryo in its young stages, since it does not become finally absorbed until the embryonic tissues have acquired considerable consistency, and so would no longer require such protection. Thus *P. novæ-zealandiæ* seems to have acquired by an extremely simple method an external layer which serves at once the double purpose of nourishing and protecting the embryo in its young stages.

A somewhat similar result is also brought about, although the means by which it is effected are quite different, in those insects which undergo an internal development, and in which the embryo is completely embedded in the yolk. The method of effecting this is considerably simpler in *P. novæ-zealandiæ* than in these insects, nothing corresponding to the amnion being present. It is possible that the amnion is a late development, acquired for the protection of the embryo, and that on its establishment it became involved with the external nutritive mass. However this may be, it is clear that there are various modes existing in Arthropods for the protection of the embryo and the nutrition of the ectoderm, and that these differ very largely in their mode of origin and in their structure, although they resemble one another in their physiological functions.

With regard to the small round bodies, which are so conspicuous a part of the peripheral layer, I have, as was said before, no definite knowledge as to their origin. From their form and structure one would be inclined to believe them to be derived from the yolk, but this is militated against by the fact that they stain a very deep red, whereas the yolk-spheres stain bright yellow, and it is difficult to imagine that some of the

yolk-spheres should suddenly change their properties towards staining reagents. The only other possible mode of origin for them is from the nuclei, which are present throughout the egg at the stage before these bodies are present. If this is the correct solution the nuclei must have been broken down and considerably altered before they were converted into their present form, since in the latter they are much smaller, instead of being granular they are homogeneous and highly refractive, and they stain much more deeply. Whatever their origin may be, they are undoubtedly an important factor in the nutrition of the egg, as they are found very plentifully scattered in the ectoderm in the comparatively early stages, and are afterwards absorbed without leaving a trace.

Mode of Formation of the Posterior End of the Embryo.—As was said in the descriptive part of this paper, I am unable to state with certainty the exact method by which the posterior end of the embryo is formed out of the egg; but however this may be effected, the condition attained in which the yolk contained in the anterior and posterior portions are separated only by a single thin layer of protoplasm is very remarkable, since at that stage the embryo possesses no definite ventral ectoderm, the ventral surfaces of the anterior or posterior halves being so closely applied to one another that the single protoplasmic septum belongs equally to each, and cannot be referred to one more than to the other.

In no other known type of development, so far as I know, does any process similar to this occur. It seems to have been acquired as a part of the peculiar crystallising-out process mentioned before as constituting one of the characteristic features in the development of this creature. It is no doubt a simple method for the formation *in situ* of the embryo, since it involves no doubling or growth in length within the egg; also, owing to the large space occupied by the peripheral nutritive layer, the amount of room within the egg is limited at this stage, and it would not be possible for the embryo to grow to any extent in length, so that the production of a doubled-up embryo *in situ* from a single embryonic mass



would doubtless be an easy and rapid mode of formation. It is not until after the peripheral nutriment has been mainly absorbed, so that the amount of space within the egg-shell is increased, that the posterior part of the body loses its close adherence to the anterior, and the embryo begins to straighten out. Also, apart from the space occupied by it, the peripheral yolk would probably act as a resistant force against a normal lengthways growth of the embryo. Ganin, in his account of the development of *Platygaster*, referred to above, describes a process whereby a result somewhat similar to that effected in *P. novæ-zealandiæ* is brought about:—the embryo after the segmentation is completed consists of a solid mass of cells, the peripheral layer being distinguished from the central mass by their more columnar form. An invagination of the ventral surface then occurs, forming a deep transverse fissure extending about half way across the embryo, and dividing it into an anterior cephalothoracic and a posterior caudal portion. So that at this stage the embryo has much the same characters as that of *P. novæ-zealandiæ* after the anterior and posterior regions of the body have acquired their own ventral walls and have become definitely distinct from one another. The stage in which the two are separated only by a single septum does not appear to possess any parallel in the development of *Platygaster*. But, apart from this, the formation in situ of an embryo doubled upon itself from a primitively single and solid mass is very remarkably similar in the two cases. It would appear to have been acquired as a simple process, the conditions being, in the fact of the enclosure of the embryo in a peripheral layer, somewhat similar in both ova.

Origin of the Endoderm.—As I said in my remarks on the segmentation, the first endodermal nuclei seem to arise by a process of free nuclear formation. The same may perhaps be the case with the later endodermal nuclei, since in no case have I found any trace in them of karyokinetic figures, which latter are extremely common in all the other nuclei. At the stage before the embryo is definitely formed, when the flattened protoplasmic plate is present along one side of the egg, there

are a few nuclei present in the central yolk, and these probably are the early endodermal nuclei. At the stage when the embryo is first definitely formed, and lies as a sac within the peripheral layer, there are nuclei present within the body of the embryo; these are irregular angular bodies with a granular structure, scattered irregularly in the central yolk, often containing one or two chromatin particles; their boundary is often indistinct, so that the nuclear passes imperceptibly into the protoplasmic substance. Later, the endoderm nuclei are much more numerous, and are arranged round the periphery of the yolk in a regular manner. Since in no case whatever at any stage have I found the least trace of any karyokinetic figures in these endodermic nuclei, and as also I often find in the central yolk all stages, from small masses of chromatin up to definite, large, fully-formed nuclei, I am inclined to believe that they arise by a process of free nuclear formation, and that no nuclear division takes place, at all events, till after the stage at which the endoderm is present as a definite layer at the periphery of the central yolk mass.

#### SUMMARY.

1. The ripe ovum of *P. novæ-zealandiæ* is very heavily charged with food-yolk, which causes it to be of comparatively large size.

2. The segmentation is on the centrolecithal type; the protoplasm is mainly at one pole of the egg, and in this protoplasm nuclei arise, probably by the division of the original segmentation nucleus. The protoplasm forms a loose reticulum containing nuclei on the surface of the egg, which first extends over only a small area, but later spreads over the surface, until in the latest stage which I have, it covers about half the periphery of the egg.

3. In the latest segmenting ova there are small masses of protoplasm in the centre of the egg; occasionally one of these may contain a nucleus, and in one case three chromatin masses are present in one of these protoplasmic areas.

4. Shortly after the segmentation begins the yolk becomes

divided up into a number of rounded segments, which, however, bear no relation to the true segmentation.

5. The protoplasm is in the form of a reticulum, and there are no traces of cell outlines.

6. In the next stage, which I have examined after the segmentation, there is a specially marked area of reticulate protoplasm, containing a large number of nuclei extending through about one third of the length of the ovum, and having in transverse section an irregular triangular shape, the base of the triangle resting on the surface of the egg. Nuclei are present throughout the whole of the yolk, being more numerous at the periphery than at the centre.

7. The triangular-shaped protoplasmic area becomes more compact and flattens itself out, forming a plate-like mass of protoplasm densely packed with nuclei on the surface of the egg. Its lateral edges turn slightly inwards away from the periphery. The nuclei over the rest of the egg have undergone no change.

8. The embryo is present as a closed sac, the walls of which are separated from the vitelline membrane by a thick layer of yolk, in which small round, highly refractive bodies are present. The embryo is enclosed in a thin layer of protoplasm, with nuclei, which represents the ectoderm. Along one line, in a longitudinal direction, there is a prominent ridge on the outer side of the ectoderm, composed of proliferating nuclei. Anteriorly this ridge divides into two, which remain attached to one another above and below, in such a way as to enclose a cavity between them.

9. At the next stage the rudiments of the præoral lobes are present in the form of a thickened mass of cells at the ventrolateral corners of the embryo. At a very short distance from the anterior end of the embryo the yolk is divided by a protoplasmic septum, which runs in a longitudinal horizontal direction, and separates the body of the embryo into two sacs, one lying above the other. The septum stops short at a short distance from the posterior end, so that the two sacs communicate freely round its end. At the regions where the septum joins the body

wall on each side of both sacs there is a thickening of the cells, which is the rudiment of the mesoderm. The peripheral yolk is mostly absorbed, but the small round bodies are still present in large quantities before, outside the embryo, and among its cells.

10. The septum has become divided into two layers by a process of ingrowth of the surrounding tissue, so that each sac is completely enclosed by a protoplasmic layer, and the embryo now consists of a sac doubled on itself in such a way that the ventral face of the anterior part of the body is opposed to that of the posterior part of the body. Indications of cavities have appeared in the mesoblastic bands, which are the rudiments of the somites.

11. The embryo begins to straighten itself out, the ventral surface of the posterior end gradually removing itself farther from that of the anterior. The mouth is present as an invagination of ectoderm on the ventral surface just behind the præoral lobes. The endoderm is present as a layer of nuclei surrounded by a reticulum of protoplasm lying at the periphery of the yolk. The somites are present in the anterior region in the form of a series of definite cavities at the sides of the body. The small round bodies outside the body of the embryo are almost entirely absorbed.

12. The embryo is still further straightened out, so that the only indication of the doubling is in the fact that the posterior end of the body is bent up at an angle to the anterior. The anus is not yet formed. The somites are present throughout the whole length of the embryo, and in the anterior ones the somatic wall is thicker than the splanchnic.

13. The peripheral food material is completely absorbed, so that the embryo lies just within the vitelline membrane and egg-shell. The appendages begin to appear as blunt rounded protuberances on a lateral ridge which runs along each side of the body. The antennæ arise as buds on the præoral lobes. The anus is present, situated on a papilla at the posterior end of the body, and consisting of a simple ectodermic invagination. A primitive streak and groove are present, anterior to and on



the dorsal side of the anus. The central yolk mass is much reduced in bulk. The somatic wall of the somites is much thickened, and in the anterior segments pushes out the ectoderm covering it, so as to form the leg portion of the somite; a small ventral outgrowth represents the rudiment of the nephridial duct. The ectoderm over the leg ridges is thickened, and at the internal ventral angles of this thickening there are special rounded elements which are the origin of the nerve-cords. The cerebral lobes of the nervous system are joined together in front of the mouth by a cerebral commissure.

In conclusion, I wish to express my thanks to Mr. Sedgwick for his kindness in providing me with my material, and for the assistance which he has given me throughout my work.

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## EXPLANATION OF PLATES XII, XIII, XIV, XV and XVI,

Illustrating Lilian Sheldon's paper "On the Development of  
*Peripatus novæ-zealandiæ*."

### *List of Reference Letters.*

*an.* Anus. *Ap.* Appendage. *At.* Antenna. *br.* Brain. *Cer. Com.* Cerebral commissure. *Ch.* Chorion. *Ec.* Ectoderm. *End.* Endoderm. *L. S.* Leg portion of somite. *M.* Mouth. *Mes.* Mesoblast. *n.* Nucleus. *n. d.* Nephridial duct. *n. s.* Nerve cord. *Ph.* Pharynx. *Pm.* Protoplasm surrounding nucleus. *Pm. A.* Protoplasmic area. *Pm. S.* Protoplasmic segments. *p.* Cavity in proliferating mass of nuclei. *p. n.* Proliferating mass of nuclei. *p. o. l.* Præoral lobe. *post. Em.* Posterior end of embryo. *pr. g.* Primitive groove. *pr. st.* Primitive streak. *p. y.* Peripheral yolk. *S.* Somite. *Sep.* Septum between the two cavities. *So.* Somatic wall of somite. *Sp.* Splanchnic wall of somite. *St.* Stomodæal invagination. *V. m.* Vitelline membrane. *Y.* Yolk in the embryo. *Y. S.* Yolk segments.

All the figures, except Nos. 23, 24, 25 and 26, were drawn with Zeiss's camera lucida; the power under which it was drawn is stated after the description of each figure.

FIG. 1.—Transverse section through an unsegmented ovum, in which the nucleus is at some little distance from the periphery. The yolk is unsegmented. *n.* Nucleus. *Y.* Yolk. *Pm.* Protoplasm surrounding the nucleus. Oc. 2, obj. B.

FIG. 2.—Section through a small portion of an unsegmented ovum, showing the nucleus situated close to the periphery. *n.* Nucleus. *Pm.* Protoplasm surrounding the nucleus. *Y.* Yolk. *V. m.* Vitelline membrane. *Ch.* Chorion. Oc. 2, obj. D.

FIGS. 3*a* and 3*b*.—Transverse sections through an ovum, in which two nuclei are present, and in which the yolk has not begun to segment.

Fig. 3*a* passes through one nucleus, which is situated at the periphery of the egg, and has a lobed form.

Fig. 3*b* passes through the other nucleus, which is at the same pole as that in Fig. 3*a*, but lies deeper in the egg. It is in a state of division, the section passing transversely through the spindle. *n.* Nucleus. *Pm.* Protoplasm surrounding the nucleus. *Y.* Yolk. Oc. 2, obj. B.

FIGS. 4*a*—*c*.—Three transverse sections through an ovum containing three nuclei, and in which the yolk has begun to segment.

FIG. 4*a* shows the whole egg. At one pole a round nucleus is present, and the yolk has begun to segment, the yolk-spheres at that pole being smaller than over the rest of the egg. Oc. 2, obj. CC.

Fig. 4*b* shows only the pole of the egg containing the second nucleus and the yolk segmentation. The nucleus is much lobed. Oc. 2, obj. D.

Fig. 4*c* passes through the third nucleus, and shows only a small portion of the egg. The nucleus is lobed and very irregular in shape. *n.* Nucleus. *Pm.* Protoplasm surrounding the nucleus. *Y.* Yolk. *Y. S.* Yolk segments. Oc. 2, obj. D.

FIG. 5.—Transverse section through the protoplasmic pole of the ovum, which is shown in surface view in Fig. 24. The protoplasm is seen to consist of a reticulum, in which the nuclei lie irregularly. *n.* Nuclei. *Pm.* Protoplasm. *Y. S.* Yolk segments. Oc. 2, obj. CC.

FIG. 6. Section through a small portion of the protoplasmic pole of the same egg as Fig. 5, highly magnified, to show the irregular arrangement of the nuclei, twelve of them being closely packed together in a small reticulate area of protoplasm. Oc. 4, obj. E.

FIG. 7*a*.—Transverse section through the protoplasmic pole of an ovum, slightly older than that from which Figs. 5 and 6 were drawn, showing how the protoplasm has spread over a larger portion of the surface of the egg; it still forms a perfectly continuous reticulum. Oc. 2, obj. D.

FIG. 7*b*.—Section through the same ovum near the limit of the protoplasmic area, to show how the protoplasmic areas are connected together by strands. Oc. 2, obj. D.

FIG. 8.—Transverse section through the protoplasmic pole of an ovum, in which the protoplasm extends over a larger area of the surface of the egg than it did in the preceding figures. The protoplasmic segments are rather more distinct from one another than they were in the preceding figures, but are still connected by strands. *Pm. S.* Protoplasm segments. *Y. S.* Yolk segments. *V. m.* Vitelline membrane. *n.* Nuclei. Oc. 2, obj. D.

FIG. 9.—Section through half of an egg of about the same stage as that shown in Fig. 8, in which the protoplasmic segments are more distinct from one another than is usually the case. *n.* Nuclei. *Pm. S.* Protoplasmic segments. *Y. S.* Yolk segments. *V. m.* Vitelline membrane. Oc. 2, obj. CC.

FIG. 10.—Transverse section through an egg, in which the protoplasmic segments have extended fully half-way round the periphery. The protoplasmic areas are separated from one another by considerable tracts of yolk; one area lies quite at the surface, and contains a large round nucleus which appears to be about to divide. Three protoplasmic masses are present in the central yolk, one of which contains three chromatin particles. The yolk does not appear to be segmented, but this may be due to the action of reagents. This figure was compounded from two sections. *Pm. S.* Protoplasmic segments. *Y.* Yolk. *n.* Nuclei. Oc. 2, obj. CC.

FIG. 11.—Transverse section through the middle of an ovum, in which there is a special area of protoplasm at one pole forming a reticulum, in which many nuclei lie. Nuclei are also present scattered through the yolk. The yolk is segmented. *Pm. A.* Protoplasmic area. *Y. S.* Yolk segments. Oc. 2, obj. A.

FIG. 12.—The protoplasmic area of the ovum shown in Fig. 11, more highly magnified, to show the reticulate arrangement of the protoplasm, the absence of cell outlines, and the irregular arrangement of the nuclei. Oc. 2, obj. D.

FIG. 13.—Transverse section of an ovum, rather older than that from which Fig. 11 was drawn. The protoplasmic area (*Pm. A.*) has become more compact and flattened. The nuclei in the rest of the egg are more numerous round the periphery than in the centre. The ovum is broken at two points. *Pm. A.* Protoplasmic area. *V. m.* Vitelline membrane. Oc. 2, obj. A.

FIG. 14.—The protoplasmic area shown in Fig. 13, more highly magnified, to show the absence of cell outlines. Oc. 2, obj. D.

FIGS. 15*a-d*.—Four transverse sections through the youngest ovum, in which the embryo is definitely formed. *Ec.* Ectoderm. *p.* Cavity in the proliferating mass of nuclei. *p. n.* Proliferating mass of nuclei. *p. y.* Peripheral layer of yolk. *V. m.* Vitelline membrane. *Y.* Yolk within the embryo. Oc. 4, obj. A.

Fig. 15*a*. Section through the anterior end of the ovum, in front of the embryonic region, showing the segmented condition of the peripheral yolk in this region.

Fig. 15*b*. Section through the anterior part of the embryonic region, showing the embryo surrounded by the peripheral yolk layer.

Fig. 15*c*. Section through the middle of the embryonic region, showing the embryo surrounded by the peripheral yolk and enclosed in the ectoderm, on one point of which is the proliferating mass of nuclei. The small round bodies are shaded very dark.

Fig. 15*d*. Section through the posterior end of the embryo, shortly anterior to its termination and behind the region of the proliferating ridge.

FIG. 16.—Shows a group of the small round bodies of the peripheral yolk layer from the embryo shown in Figs. 18*a—c*, highly magnified. They are vacuolated. Reichert's  $\frac{1}{15}$  oil immersion.

FIGS. 17*a—c*.—Three sections through an embryo, somewhat older than that from which Figs. 15*a—d* were drawn. *Ec*. Ectoderm. *Mes*. Mesoblast. *p. o. l.* Præoral lobes. *post. Em.* Posterior tip of the embryo. *Sep.* Septum. *V. m.* Vitelline membrane. Oc. 4, obj. A.

Fig. 17*a* is a somewhat oblique section through the anterior end of the ovum. It passes through the posterior tip of the embryo (*post. Em.*), which is distinct from the ventral wall of the anterior end, being surrounded by a complete layer of ectoderm. Owing to the obliquity of the section the right præoral lobe is considerably larger than the left.

Fig. 17*b* is through the middle of the ovum, where the anterior and posterior ventral surfaces of the embryo are only separated from one another by a single protoplasmic septum (*Sep.*)

Fig. 17*c* is through the hind part of the egg, behind the region of the septum, where the anterior and posterior portions of the embryo are in free communication with one another.

FIGS. 18*a—c*.—Three transverse sections through an ovum, rather older than that figured in Figs. 17*a—c*. *Ec*. Ectoderm. *Mes*. Mesoblast. *p. o. l.* Præoral lobes. *p. y.* Remains of peripheral yolk. *S.* Somites. *St.* Stomodæal invagination. *V. m.* Vitelline membrane. *Y.* Yolk. Oc. 3, obj. A.

Fig. 18*a* passes through the anterior end of the embryo, in the region of the præoral lobes. The ectoderm has begun to invaginate in the middle ventral line to form the stomodæum, and the somites of the præoral lobe segment are present (*S. 1.*). The space between the embryo and the vitelline membrane is occupied by a large number of the small round bodies, which are also present among the tissues of the embryo.

Fig. 18*b* passes through the middle of the ovum. The ventral surfaces of the anterior and posterior regions of the body are completely separate from one another. The somites (*Sep.*) of the trunk are beginning to appear (*S.*)

Fig. 18*c* passes through the hind of the embryo, where the anterior and posterior portions of the embryo are continuous.



FIGS. 19*a—d*.—Four rather oblique transverse sections through an ovum, in which the embryo is still doubled on itself, though rather less so than in the ovum from which Figs. 18*a—c* were taken, and the space between the apposed ventral surfaces is greater. In this ovum the endoderm is first definitely differentiated as a distinct layer. A few small round bodies are still present between the vitelline membrane and the ectoderm, but most of them have by this time been absorbed. *Cer. Com.* Cerebral commissure. *Ec.* Ectoderm. *End.* Endoderm. *M.* Mouth. *Mes.* Mesoderm. *p. o. l.* Præoral lobes. *post. Em.* Posterior tip of the embryo. *S.* Somite. *V. m.* Vitelline membrane. Oc. 3, obj. A.

Fig. 19*a* passes through the anterior end of the embryo in front of the mouth, in the region of the cerebral commissure.

Fig. 19*b* passes through the mouth of the embryo. The posterior tip is shown lying on the ventral side of the ovum, separated by a considerable space from the mouth.

Fig. 19*c* is from a section posterior to the above. It passes through the anterior part of the embryo behind the mouth, on one side passing through the posterior end of the præoral lobe; and through the posterior part of the embryo in the region behind that where the somites are present, the mesoblast (*Mes.*) being solid.

Fig. 19*d* passes through the posterior end of the ovum, in the region where the anterior and posterior portions of the embryo are continuous with one another.

FIG. 20.—Transverse section through an embryo which has become almost completely straightened out. The somatic wall (*So.*) of the somites is thickened, as also is the ectoderm lying over it. *End.* Endoderm. *n. s.* Rudiments of ventral nerve-cords. *S.* Somite. *Sp.* Splanchnic wall of somite. *So.* Somatic wall of somite. Oc. 4, obj. A.

FIGS. 21*a—c*.—Three transverse sections through the embryo, which is shown in surface view in Figs. 25 and 26. *an.* Anus. *Cer. Com.* Cerebral commissure. *End.* Endoderm. *br.* Brain. *L. S.* Leg portion of the somite. *n. d.* Rudiment of nephridial duct. *n. s.* Ventral nerve-cord. *Ph.* Pharynx. *S.* Somite. *Sp.* Splanchnic wall of somite. *So.* Somatic wall of somite. Oc. 4, obj. A.

Fig. 21*a* is taken just in front of the mouth, in the region of the cerebral commissure. The pharynx is seen in communication with the gut.

Fig. 21*b* passes through the appendage of the left side, and shows the somite dividing into a leg and a body portion, and also the ventral outgrowth which will form the nephridial duct.

Fig. 21*c* passes through the anus, and the lateral ridge behind the region, where it is divided into appendages.

FIG. 22.—Shows the primitive streak, and is taken from a section a little

posterior to that shown in Fig. 21*c*, but it is more highly magnified. *End.* Endoderm. *pr. g.* Primitive groove. *pr. st.* Primitive streak. *Oc. 2, obj. D.*

FIG. 23.—Surface view of a segmenting ovum, to show the yolk segmentation. *Ch.* Chorion. *Y. S.* Yolk segments.

FIG. 24.—Surface view of a segmenting ovum. The protoplasmic segments are seen lying on the surface of the egg. The yolk segmentation is not seen, owing to the surface of the egg having been slightly disintegrated by the preserving reagents. The chorion and vitelline membrane have been removed.

FIG. 25.—An embryo, in which all the peripheral nutritive layer has been absorbed, viewed from the side; showing the large præoral lobe with the antenna budding out from it, and the lateral ridge with five distinctly formed appendages (*Ap.*).

FIG. 26.—The same embryo seen from the ventral side, and showing the mouth and anus and primitive groove, in addition to the structures seen in the last figure. These two drawings were from an embryo preserved in picric acid. *an.* Anus. *Ap.* Appendages. *At.* Antennæ. *M.* Mouth. *p. o. l.* Præoral lobe. *pr. gr.* Primitive groove.



## On Some Points in the Anatomy of Polychæta.

By

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With Plates XVII, XVIII and XIX.

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### 1. NEPHRIDIA AND GONADS.

BEFORE the year 1880 it had been conclusively shown by the results of various researches that a "segmental organ" was a glandular tube, either simple or convoluted, ciliated through the greater part of its length, having internally a ciliated funnel-shaped opening by which it communicated with the body cavity, externally an opening to the exterior. The function of the segmental organ had been shown to be excretory, depurative, but it had also been proved that in some cases at least the organ served as efferent duct for the reproductive elements. The segmental organs in their typical form had been found principally in the Chætopoda, but it had been shown that the tubular glands known as the "Organs of Bojanus" in Mollusca conformed in all essential features to the plan of a segmental organ, though they did not as a rule act as genital ducts.<sup>1</sup> Notwithstanding that these facts had

<sup>1</sup> The generalisation that excretory tubes similar to "segmental organs," were homologous structures in whatever division of the animal kingdom they occurred, was formulated by Lankester in 1877, in his "Notes on Embryology and Classification," published in this Journal. To the morphological element so defined he gave the name Nephridium, as applicable in every case. This view of the original morphological identity of excretory organs was confirmed by the discovery of typical nephridia in *Peripatus*, which was made by



been firmly established as important landmarks in zoology, in the year I have mentioned appeared a memoir bearing the name of L. C. Cosmovici,<sup>1</sup> in which the whole question of segmental organs was thrown into confusion. Overlooking or rather wilfully disregarding the more recent investigations which had brought to light the true relations of the segmental organs, and which had resulted in a generally applicable definition of the organs, this memoir takes the original work of Williams as a foundation, and carefully compares every case examined with Williams' original description. Because Williams did not perceive the glandular nature of the organs, but only their connection with the reproductive functions, Cosmovici defined a segmental organ as a generative duct, while a glandular tube or pouch must be considered and called an organ of Bojanus. As the real segmental organs, or as they are now called nephridia, are usually both glands and genital ducts, they were stated in this extraordinary paper to be usually compound, consisting of a glandular tube, the organ of Bojanus, and a ciliated non-glandular funnel, the segmental organ; while certain cases were described in which the primitive distinctness of the two structures was, as the author believed, retained. Perhaps the most surprising point in this phenomenal paper is that the absence of an internal or cœlomic opening is taken as characteristic of the "organ of Bojanus" in the Polychæta, and this in 1880 when to every commencing student of zoology was demonstrated the internal or cœlomic opening in the molluscan organ to which the name organ of Bojanus was originally given. It would be best if it were possible to exclude the paper of Cosmovici entirely from the

Balfour in 1879 (this Journal). The Hertwigs have argued ('Die Coelomtheorie,' 1881), that the excretory organs of Mollusca are not perfectly homologous with those of Chætopoda, Vertebrata, &c., but it has been shown that the pericardial space in Molluscs belongs to a system of mesodermic cavities, distinct from the vascular cavities, and it is pretty generally agreed now, that these mesodermic cavities in Molluscs as well as those in Phatyhelmia represent a cœlom.

<sup>1</sup> "Glandes Génitales et Organes segmentaires des Annélides Polychètes," 'Arch. Zool. Exp.,' Tom. viii.

literature of the subject with which it professes to deal, and regard it as of merely psychological interest; but the paper contains detailed descriptions and drawings of the anatomy of several forms of Polychæta, and these have been by some later writers accepted as trustworthy. In a critical paper by R. S. Bergh,<sup>1</sup> published in 1885 which reviews the relations of the nephridia in the various classes of Vermes, the facts concerning the Polychæta are mostly taken from Cosmovici's memoir. But a great many of Cosmovici's statements are quite erroneous, and although he has described other facts correctly the false is so mingled with the true, and the actual descriptions of structure are so mingled with false theoretical views, that it is not safe to accept anything in his paper without re-examination of every case.

#### *Arenicola marina*, Linnæus.

In 1868, when Claparède's 'Chétopodes du Golfe de Naples' was published the gonads of *Arenicola* were unknown. In that work it is stated that most authors had taken the nephridia to be reproductive organs, some describing them as ovaries, others as testes. Quatrefages ('Hist. Nat. des Annelés,' 1865) called the nephridia simply genital organs. Grube ('Zur. Anat. u. Phys. der Kiemenwürmer') had assured himself that the ovaries were not to be sought in these organs, for he had seen (as he thought) the ova formed on the exterior of vascular caeca of the lining of the coelom. He was inclined to regard the nephridia as testicles. This was an impossible view, because, as Claparède says, the sexes of *Arenicola* are separate, but it seemed very probable to Claparède that Grube was right as to the origin of ova, and in support of the opinion of Grube he gives a figure of one of the caecal pseudhæmal vessels surrounded by a layer of cells. Claparède then quits the question of the genital organs, and proceeds to give a not very accurate description of the nephridia in *Arenicola Grubii*, Clap. He says the organs previously described as generative organs are really segmental organs of a very peculiar structure, and are

<sup>1</sup> 'Die Exkretions-organe der Würmer Kormes,' Bd. ii, 1885.

only connected with the phenomena of reproduction as efferent ducts. There are five pairs placed in the fourth to the eighth setigerous segments. Three parts are distinguishable in each organ, the funnel, the gland, and the vascular reservoir. He describes correctly the fringed and ciliated dorsal edge of the funnel; but his account of the shape of the glandular part, which he compares to a comma, does not agree perfectly with what is seen in *A. marina*. His figures are not good, though creditable for the date at which they were made. Claparède never saw ova in the interior of the nephridia, but once saw spermatozoa in the funnel. Of *Arenicola marina*, Lin., he says merely that the segmental organs have a great analogy with those of *A. Grubii*.

Casmovici's description of the nephridia and gonads in *Arenicola marina* is correct in almost every particular; his figures of minute structure are not satisfactory, but his anatomical figures are clear and accurate; and if it were not for the absurd manner in which he has separated the nephrostomata as distinct organs from the nephridia themselves, his description would be worthy of a permanent place in zoological literature. To him, in any case, is due the credit of having been the first to discover and describe the true gonads in *Arenicola*. He states there are six pairs of nephridia, each with its external opening, and situated in the third to eighth somites. The external opening of each organ is situated close behind the upper end of the corresponding uncinigerous torus. The funnel or nephrostome is correctly described by Cosmovici; it is provided with a free membranous dorsal border, fringed and ciliated. Along this border runs a pseudhæmal vessel, a branch from the branchial artery, which is given off by the ventral vessel. (Cosmovici believes the ventral vessel to be connected with the heart, and to be arterial; it is more probably venous; that is, it probably receives the blood from the branchiæ.) The vessel which runs along the dorsal border of the nephrostome is continued diagonally backwards and outwards across the nephridium, and in this part of its course, posterior to the nephrostome, it runs through the gonad; the

tissue of the gonad is, in fact, continuous with the posterior angle of the nephrostome.

There is not, then, a great deal to be added to Cosmovici's account, but there are one or two corrections to be made, and a re-examination of the subject was necessary because the falseness of his interpretation causes his description to be received with doubt. His account of the position of the nephridia is inaccurate; they are situated in somites v—x (the fourth to ninth chætigerous) inclusive. The first or buccal somite of *Arenicola* is destitute of bristles: the following six somites bear each a dorsal fascicle of capillary chætæ, and a ventral torus uncinigerus, but no branchiæ; the next thirteen somites bear each both fascicle and torus, and, in addition, a pair of plumose branchiæ; the rest of the body, which is of different lengths in different individuals, is thinner, and devoid of fascicle, torus, and branchia; it is cylindrical and covered uniformly with papillæ. Behind the first four somites are incomplete septa. The nephrostome of the first nephridium is on the anterior face of the fourth septum. Between any two successive parapodia, behind the third, are five constrictions, of which the fifth is the deepest. The septum, when present, is attached to the body wall opposite the second constriction. Between the fifth constriction and the parapodium is a prominent ridge ending in a sharp edge. The first nephridia of the first pair are somewhat smaller than the rest. The relation of the gonad to the nephridium is shown in Pl. XVII, fig. 1, which gives a view of the internal face of the nephridium. In the natural position the nephridia are covered dorsally by the bands of oblique muscles, which pass from the sides of the nerve-cord to the line of dorsal bristles; and in this condition the dorsal lip of the nephrostome is horizontal, and its edge is directed downwards and inwards.

Cosmovici says he searched in vain for a long time for the genital organs, and discovered the ovary by accident when examining a piece of the nephridium. I discovered the ovary by tracing the origin of the ova in the body cavity. In February last I found two or three specimens which had ova in the body cavity;



in these and in others in which mature ova were not present, loose cellular masses were often seen in the neighbourhood of the nephridia. After careful search, several times repeated, these masses were traced to the cord of cellular tissue already described as attached to the nephridium; the cord of cells is merely, as usual, a local development of cœlomic epithelium. In most specimens the cells of this cord were so undifferentiated that it was not easy to be certain it was a gonad, but in specimens which contained a few ova in the body cavity young ova could be recognised in the cord. The reproductive cells leave the gonad at a very early stage of development, and reach maturity while floating freely in the body cavity.

*Cirratulus cirratus*, Malmgren (O. F. Müller).

Keferstein<sup>1</sup> in 1862 gave a slight description of the segmental organs in *Cirratulus filiformis*, Kef., *bioculatus*, Kef., and *borealis*, Lam. He made out the relations of the organs most completely in the first-mentioned species, in which he describes them as a single pair of ciliated tubes, each bent on itself, extending through segments 1 to 5, and having an internal and an external opening. He gives a figure of the organ as seen in the living animal, and the figure shows both the external and internal openings in the first setigerous or post-buccal somite. Less complete descriptions and figures are given of the organs in the other two species. No other nephridia are mentioned by Keferstein except this pair at the anterior end.

Claparède also saw but a single anterior pair of nephridia in species of *Cirratulus*. He says ('Ann. Chet. Naples'): "*C. chrysoderma*, like all the *Cirratuliens*, has only a single pair of segmental organs, opening at the second segment (first setigerous) by an oval aperture situated on the inner side of the ventral bristles. The organ is rolled in an angular spiral. Its external part is narrow, but soon enlarges suddenly into a wide ciliated tube. The internal opening has escaped me."

<sup>1</sup> 'Zeits. f. wiss. Zool.,' Bd. xii, 1862.

Cosmovici (loc. cit.) was unable to see the large anterior nephridia described by Keferstein and Claparède, but states that in *C. filiformis*, Kef., segmental organs are present in pairs in nearly all the segments, especially of the middle and posterior region: that they are attached to the anterior face of each diaphragm: the figures of this species which he gives do not show the organs mentioned. The Errantia, among which he places *Cirratulus*, according to Cosmovici's peculiar views, have only segmental organs and no organs of Bojanus, and he denies altogether that the internal opening of the segmental organ communicates with the cavity of the somite in front of the one which contains the organ itself.

In *Cirratulus cirratus* both the large anterior pair of nephridia described by Keferstein and Claparède, and the series of pairs in the middle and posterior region mentioned by Cosmovici, are present. The nephrostome of the first nephridium opens into the cavity of the buccal somite, being situated on the anterior face of the first septum, somewhat ventrally, in the angle between the septum and the lateral body wall. The proximal part of the bent tube passes backwards from the nephrostome till it reaches the second septum (Pl. XVII, fig. 3), then passes upwards to the dorsal body wall, where it opens into the wider distal part of the tube which opens to the exterior beneath the neuropodium of the second somite. The posterior nephridia are smaller and simpler; they appear first in the twelfth somite, and are repeated hence to the end of the body. Each of them has a nephrostome of the typical form, an elongated funnel with its aperture directed forwards. The nephrostome has a similar position to that of the large anterior nephridium, that is to say, it is placed in the lower external corner of the anterior face of its septum. The lips of the funnel are composed of a columnar ciliated epithelium resting on a thin fibrous membrane; this membrane is continued on the one hand into the transverse septum, on the other into the body wall; the lips of the funnel project inwards and forwards into the cavity of the somite. The nephridial tube when traced from the nephrostome (in a series of horizontal sections)

is seen to pass obliquely backwards and downwards, curving over the dorsal edge of the ventral longitudinal muscle, and opening beneath the neuropodial bristles. The internal openings of the simple nephridia are shown as seen in a horizontal section in fig. 4, while fig. 5 shows the external opening in a transverse section of a female specimen.

The simple nephridia act as efferent ducts for the reproductive elements in both sexes. I found a number of specimens distended with the genital products at the end of March in the current year, lying under stones on the banks of Granton Quarry, where they are pretty abundant at all seasons. These, when placed in a basin of sea-water, commenced to shed eggs and spermatozoa. The ova were fastened together, after their escape, by transparent gelatinous mucus, which formed a soft mass without any definite shape adhering to the stones and mud among which the worms were lying. The escape of the ova could be observed without much difficulty.

Fig. 6 shows the appearance presented by two somites of the worm viewed under a low power by reflected light, as the ova were escaping; the apertures seen are the openings of the simple nephridia previously described. In sections of a male specimen these nephridia are seen full of spermatozoa. The larger nephridia of the second somite do not, as far as I have been able to ascertain, transmit the sexual products; indeed, no ova (or spermatozoa) are produced in the first eleven somites where simple nephridia are absent.

I have not discovered in my sections any satisfactory indication of the places where the germinal cells are developed; the position of the gonads is doubtful. The reproductive cells undergo the greater part of their development in the body cavity. The presence of a complete longitudinal vertical septum above and below the intestine in *Cirratulus* is remarkable.

#### SPIONIDÆ.—*Nerine cirratulus*, Clap.

This form has not hitherto been recorded as occurring in the North Sea, either on our own coast or other parts of

north-west Europe. It is, however, common enough between tide marks in the sand at Granton. Claparède<sup>1</sup> does not give any description of the segmental organs, he merely mentions that the ovaries are attached to them, and render their study difficult. There is, of course, no great difficulty in making out the relations of the nephridia in longitudinal and transverse sections. These relations are in some small points exceptional, and longitudinal sections are the most instructive. The nephrostome is a wide ciliated funnel, the lips of which are simple and entire, not produced into lobes. The aperture of the nephrostome is large and gaping as in *Cirratulus*. The lower lip of the nephrostome projects into the cavity of the somite, while the upper is continuous with the transverse septum, on whose front face the nephrostome lies. The nephrostome is situated at the lower and outer corner of the septum, and leads into a narrow tube, which pierces the septum and then dilates into a small spherical vesicle, which on the median side is produced into a point, and to this point the gonad is attached (fig. 7). A little more to the exterior side the vesicle gives off a long duct, which passes upwards to the body wall and opens to the exterior (fig. 8). As a general rule the efferent duct of the nephridium in *Polychæta* passes downwards ventrally, and opens below the level of the neuropodium. In *Terebellidæ* the external aperture is near the upper end of the uncinigerous torus, but in this case the ventral band of muscle extends some distance upwards, and thus, although the nephridial aperture has an exceptional position with regard to the neuropodium, it has its normal relation to the ventral muscles. In *Nerine* there is no such reason for the extremely dorsad position of the nephridial aperture; the ventral band of longitudinal muscles on each side is folded in at its borders, and the two bands occupy only the ventral surface of the transverse section; the dorsal bands in like manner occupy only the dorsal wall; the whole of the lateral region of the transverse section, which approaches a parallelogram in shape, is destitute of thick muscular bands, and the fascicles of bristles are widely sepa-

<sup>1</sup> 'Ann. Chét. du Golfe de Naples,' Geneva, 1868.



rated. The efferent duct of the nephridium is therefore not confined in a narrow space between the edges of the dorsal and ventral muscle-bands, as is usually the case, and there is no apparent reason why the duct should not pass between the ventral muscle and the neuropodial bristles as it does in most Polychæta.

It is certain that in this species the nephridia act as sexual ducts in both sexes. I have frequently seen these organs in the male distended with spermatozoa, and the ova doubtless pass out in the same way.

#### *Nerine coniocephala*, Johnston.

In this species the nephridia have the same character and somewhat similar relations to those described in the preceding, but the efferent duct is by no means so long, and the external aperture is therefore more ventral in position; it is on the same level as the upper neuropodial bristles, and lies in front of the neuropodium in the constriction between adjacent somites (fig. 9). Sections of ripe males show the lumen of the nephridium full of spermatozoa.

#### *Lanice conchilega*, Malmgren.

Several accounts of the nephridia of *Terebella conchilega* have been given. H. Milne-Edwards ('Ann. d. Sci. Nat. (2) Zoologie, x,' 1838, p. 220), in a paper published in 1838, on the circulation in Annelids, describes the vascular system in a species to which he gives this name, and gives a figure of the animal opened along the dorsal median line. In this figure four looped nephridia are distinctly shown, situated behind the branchial region. The representation of the position and character of these organs is perfectly correct, so far as it goes; they are the upper parts of the four nephridia belonging to somites VI—IX. But the paper I refer to does not describe the nephridia, as it deals with another subject: they are shown in the figure, and that is all; and in the description of the figure the organs are referred to as organs of generation.

Keferstein ('*Zeitschrift für wiss. Zoologie*,' Bd. xii, 1862) mentions that the structure and number of the nephridia in *T. conchilega* are the same as in *T. gelatinosa*, Kef.; in both cases he says there are six pairs, each organ consisting of a tube bent on itself, of which one half is darker, the other lighter; the organs belong to segments 3—9.

Cosmovici<sup>1</sup> gives an erroneous description of the organs; he says there are two pairs without internal openings, which he calls "organs of Bojanus," one of these situated in front of the cephalic diaphragm, the other immediately behind it, each organ having an external opening; and two other pairs, each of which has an internal as well as an external opening, and is shaped like an urn; the internal opening is large, and surrounded with a circular lip. The gonad is attached to the posterior part of each of these latter organs, which Cosmovici calls segmental organs, and which he says serve as efferent genital ducts.

The species referred to by these three authors is the *Nereis conchilega* of Pallas, *Terebella conchilega* of Gmelin; and this is called *Lanice conchilega* by Malmgren. My specimens were identified from Malmgren's description, and there is no doubt of their identity with the species of that author; but there is room for some uncertainty regarding the specific identity of the specimens referred to by the authors I have mentioned. For instance, Cosmovici identified his species by means of Quatrefages' '*Histoire des Annélés*,' 1865, and there it is stated that the tube of *Terebella conchilega* possesses no hollow fringes at its mouth; these fringes are always present in the tube of *Lanice conchilega*, Malmgren. This species is distinguished by some marked characters; two of them are the presence of a large vertical lobe on the third somite (second branchiferous), and the coalescence of the ventral scutes usually present into a continuous ventral plate.

The fact that in *Lanice conchilega* the nephridia of a side communicate together so as to form a longitudinal tube, has

<sup>1</sup> "Glandes génitales et Organes segmentaires des Annélides polychètes," '*Arch. de Zool. Exp.*,' t. viii, 1879-80.

been observed by Edouard Meyer of the Zoological Station at Naples ; and his discovery is mentioned by his permission in a single sentence in Lang's 'Monograph on the Polycladen,' published in 1884.<sup>1</sup> But the accessible information concerning these organs in this species is so inadequate, that R. S. Bergh,<sup>2</sup> in a general review of the excretory system in worms, cites both Lang's mention of Meyer's observation and Cosmovici's account of the organs as if they were both equally correct.

The true relations of the excretory system are as follows :— Enumerating the somites from before backwards, and counting the buccal as the first, we find that the branchiæ belong to somites II, III, and IV : the first notopodial fascicle of capillary chaetæ is on the fourth somite, the third branchiferous ; the first neuropodial uncinigerous torus is on the fifth ; the neuropodial tori are repeated on every succeeding somite to the end of the body ; the notopodial fascicles occur only on seventeen consecutive somites. There are traces of transverse septa behind the first, second, third, and fourth somites, but none in the rest of the thoracic region, which bears the notopodial fascicles. On dissection, four long double nephridial tubes are seen projecting dorsalwards into the body cavity ; the lower parts of these tubes are covered by strands of the oblique muscles which pass from the nerve-cord to the neighbourhood of the notopodial bristles ; careful examination shows that these tubes belong to somites VI, VII, VIII, and IX. Their internal openings can be found immediately behind the fascicle of bristles belonging to somites V, VI, VII, and VIII respectively, but their efferent tubes are seen to pass down beneath the fascicle of somites VI, VII, VIII, and IX. The lower parts of these efferent tubes are very wide, and it is impossible to separate them from one another. Beneath the fascicles of the following four somites (X to XIII inclusive) are seen membranous nephridial sacs, which externally at least are inseparable from one another. These sacs are simple, that is, they are not composed of a tube bent on itself like the anterior nephridia ; they scarcely extend above the level of the oblique muscles, and

<sup>1</sup> 'Fauna u. Flora des Golfes von Neapel,' xi Monographie.

<sup>2</sup> 'Die Exkretions-organe der Würmer' Kosmos, Bd. ii, 1885.

no internal opening or nephrostome can be found in them. In front of the most anterior nephridium, that belonging to somite VII, are seen traces of a rudimentary nephridium (see fig. 10). In order to trace out the relations of these nephridia more accurately, the anterior part of a specimen was cut into a series of horizontal longitudinal sections commencing with the ventral surface, and the reason why the successive nephridia could not be isolated from one another was seen on examination of these sections; the lower parts of the efferent limbs of the four anterior normal nephridia, in somites VI to IX, and the whole of the nephridial sacs in somites X to XIII are in open communication, forming a wide continuous longitudinal tube extending from somite VI to somite XIII (see figs. 11 and 12). Openings to the exterior from this tube were found in somites VI to IX inclusive, corresponding to the four large looped nephridia; each of these openings was close behind the upper end of an uncinigerous torus. The internal openings of the same four nephridia could be traced with ease and certainty; they are attached to the body wall close behind the notopodial fascicles of somites V to VIII. These openings are wide, and are overhung dorsally by a longitudinal lip furnished with a series of small ciliated digitate processes; lower down, the anterior and posterior lips of the opening are simple, thick-walled, and ciliated. The aperture leads into a thin tube, which passes inwards and backwards, curving round the inner end of the fascicle of bristles behind the aperture, and then, crossing the continuous tube, passes up on the inner or mediad side of the loop, at the apex of which it is continued into the efferent wider limb of the loop, which passes down on the outer side to open into the longitudinal tube. Neither internal nor external openings could be found in that part of the longitudinal tube which is behind the loops; it seems evident that this part of the tube represents four somewhat reduced nephridia which have coalesced, but whose openings have disappeared. Anteriorly to the four looped nephridia are traces of three others; the longitudinal tube extends forwards into somite V as if it included a nephridium belonging to that somite, but I could find



no external opening in this somite; at the angle between the septum behind somite iv and the body wall is a very obvious nephrostome, which ought to lead into the longitudinal tube, into that part of it corresponding to somite v, but the connection could not be traced. Nephrostomes were also present attached to the anterior face of the septa behind somites ii and iii (the first and second branchiferous), and leading into tubes seen in somites iii and iv, but I could find no external openings in these somites. I could find no nephrostome in somite i (the buccal), nor any trace of a tube in somite ii. Gonads are present in the form of clumps of deeply-staining, small, indifferent cells, attached to the exterior of all the nephrostoma mentioned, seven in all (see fig. 13). The germinal cells, when still quite undifferentiated, separate from the gonads, and undergo further development in the cœlom. But I found no reproductive elements in the cavity of the nephridial system, though the body cavity contained them in quantity, and it is probable that at the right season they are expelled through the nephridial cavities. The body cavity contains, besides the reproductive elements, a large number of spherical, vacuolated, nucleated cells. This is the only case in which a communication between successive nephridia has ever been discovered in any adult invertebrate. It is true that in the development of *Polygordius*, according to Hatschek, each nephridium gives off backwards a prolongation of itself, from which the next nephridium is formed, and the two remain in communication for a time; but the connection is soon severed, and in the adult the successive nephridia are isolated and independent. In *Lanice conchilega* the nephridia have coalesced together after coming in contact from before backwards, the separating membranes having disappeared. The case is extremely interesting in the fact that we have in it an approximation to the condition of the excretory system in Vertebrata; the presence of a metameric series of nephrostomata in vertebrate embryos has long ago been seen to constitute a resemblance between them and Chætopoda, but no other Chætopod is known which resembles the verte-

brate in having a number of nephridia coalesced to form a continuous longitudinal tube.

It is surprising to find that, as far as I have been able to discover, no resemblance to the condition seen in *Lanice conchilega* occurs in any of its near allies. The only species of the genus *Terebella* as defined by Malmgren that occurs in the Firth of Forth is *Terebella Danielsseni*, but of this I have only one specimen, and have not examined its nephridia. Of *Amphitrite* there are two species in the Forth; *Amphitrite cirrata* I have not examined anatomically; in *Amphitrite Johnstoni* there are a large number (fifteen to seventeen) of nephridia forming long loops projecting dorsalwards into the body cavity in the anterior region; each has its own internal and external openings, and is isolated and independent. In *Terebellides Strœmi* there is one pair of large dark-coloured nephridia in the anterior end, and three pairs of small rudimentary ones posterior to this.

In *Pectinaria belgica* there are three pairs, all independent; they are described in the following section. In *Melinna cristata* there are several pairs all separate.

#### *Pectinaria belgica*, Lamarck (Pallas).

Mr. Harvey Gibson<sup>1</sup> has by carefully neglecting the distinguishing differences between this species and *Amphitrite auricoma*, Müller, attempted to prove that the two forms are identical. He points out that in the original figures of Pallas, of *Nereis cylindraria*, var. *belgica*, "the stiff golden comb shows one continuous and uniform series of teeth, not two series as in *P. auricoma*," and that figures by subsequent authors, e.g. M'Intosh and Malmgren, show the two combs in *P. belgica* with perfect distinctness. Moreover, certain references in Pallas's text imply that his species had two distinct combs. Mr. Harvey Gibson concludes that "either Pallas's draughtsman made an error in most of the figures of *P. belgica*, and failed to represent the comb with sufficient

<sup>1</sup> "Notes on some of the Polychæta," 'First Report on the Fauna of Liverpool Bay,' Lond., 1886.

accuracy, hence leading Müller into error when comparing his form with that of Pallas; or Pallas's figures are correct (although his references in the text are wrong), and his species is distinct from that of Müller (for the condition of the comb appears to be the only important difference between the two). Looking at the inaccuracy of the drawings as compared with var. *capensis* in Pallas's work, and taking into account the indistinctly double series of teeth shown in figs. 5, 8, and 9 of var. *belgica*, I think that probably the former view is most likely to be the correct one. In that case *P. auricoma* of Müller disappears, and becomes *P. belgica* of Pallas." How a zoologist, after actually referring to the description and figures given by Müller of *Amphitrite auricoma*, and to the description and figures of both species given by Malmgren in his 'Nordiska Hafs-Annulater,' could suppose the condition of the comb to be the only important difference between the two, it is difficult to understand. The two distinguishing features given by Müller are (1) the curvature of the tube; (2) the serration of the margin of the flattened area behind the palmulæ. Malmgren mentions both these characters and figures them, and he examined specimens of both species; only Malmgren made the two characters generic instead of specific, and called Müller's species *Amphictene auricoma*. We can state with certainty that in our specimens the tube is perfectly straight, and the margin of the post-palmular area perfectly entire. The presence of two distinct palmulæ, as Mr. Harvey Gibson would have seen if he had studied the Latin descriptions of Malmgren, is common to the whole family *Amphictenea*.

There are three pairs of nephridia in *Pectinaria belgica*, of which the first are the largest; all the organs are of the usual type, each consisting of a tube bent upon itself and provided with a nephrostome and an opening to the exterior. There is a transverse septum separating the buccal somite from the following; the nephrostome of the first nephridium is on the anterior side of this septum. The nephridia are brown or black in colour. The tube of the first reaches dorsalwards

above the intestine, and its external opening is a little ventral to the origin of the first branchia. Between the nephridial opening and the root of the branchia is the aperture of a peculiar glandular organ whose function we have been unable to ascertain. On dissection of a fresh specimen this gland is seen as a milk-white, opaque, cylindrical body about one eighth of an inch long, free everywhere except where it is continuous with the body wall round its opening to the exterior. The efferent duct of this gland is lined by a high columnar epithelium, of which the component cells are solid and columnar; throughout the rest of the gland there is a layer of long solid nucleated cells next to the basement membrane, but these are covered by other layers of large vacuolated cells whose walls form a network nearly obliterating the lumen of the organ. The wall of the gland is well supplied with pseud hæmal vessels. The third somite (i. e. second branchiferous) and the fourth are unprovided with nephridia, but the latter contains a nephrostome belonging to the nephridium of the fifth somite; the sixth somite is likewise provided with a nephridium whose nephrostome is in the fifth somite. The nephrostomata are simple elongated funnels with their apertures directed forwards; they are not provided with such a series of digitate processes as is seen in *Lanice* and *Arenicola*. The gonads are of the usual type, masses of undifferentiated cells attached to the exterior of the nephrostomata on the mediad side. The reproductive cells become detached at a very early stage and pass through the rest of their development in a free condition in the cælom. It is certain that the spermatozoa reach the exterior by passing through the nephridia; in a series of sections of a ripe male I saw the nephrostomata and nephridial tubes distended with them. Between the two posterior nephrostomata and the body wall pass membranes, which are rudiments of transverse septa. There is also a rudiment of a septum between the second and third somites (first and second branchiferous). The external apertures of the two posterior nephridia are ventral and posterior to the notopodial setæ of their somites.



*Nereis virens*, Sars.

Claparède did not study the nephridia in the *Nereidæ*. Ehlers<sup>1</sup> has given a description of the organs as he saw them in *Nereis cultrifera*, Grube, and other species. He says the segmental organ lies close behind the entrance into the cavity of the parapodium, on the inner surface of the ventral body wall, near the lateral border of the ventral muscular band: that it consists of an easily noticed, almost spherical body, and an efferent duct, which runs on the ventral body wall towards the hinder border of the segment, where it opens to the exterior: that the body of the segmental organ in a large epitokous female of *N. virens* was .189 mm. by .108 mm. in size. In the inside of the body of the organ he states there were a number of clear cavities, which, when the organ was compressed, were discovered to be portions of a continuous convoluted canal which was embedded in the mass of the organ; the inner surface of the walls of this canal was ciliated. On the upper surface of the body of the organ was a slightly curved, cleft-like aperture, with thickened edges, which carried cilia; this cleft was the internal opening of the organ; on the opposite side of the spherical body the thin efferent duct passed off. Ehlers concludes his description thus: "In support of the view expressed by myself, that the segmental organs serve as efferent ducts for the sexual products, I may point to the fact observed by me that these organs in *N. virens* contained perfectly mature ova, which were found in the efferent duct of the organ as well as in its body, and that not seldom a single ovum lay in the external aperture." Ehlers gives a figure of an isolated segmental organ which corresponds fairly well with his description.

But that description is erroneous in one important point. The segmental organ or nephridium in *Nereis virens* does consist of a somewhat spherical mass composed of a number of glandular ciliated tubes, which probably all form a single convoluted tube, and a straight, thin, efferent duct, passing off

<sup>1</sup> 'Die Berstenwürmer,' 1864—1868.

from the spherical mass to open to the exterior on the ventral side of the base of the parapodium. But the internal aperture, the nephrostome, is not a cleft such as Ehlers figures and describes in the wall of the spherical mass. The nephrostome is situated at the end of a simple thin ciliated tube, which projects out from the spherical body at the side opposite to the efferent duct. The nephrostome is funnel shaped, as usual, but the edges of the funnel are produced into numerous finger-like lobes, and from the lobes project a forest of delicate, pellucid, branched processes, the surface of which is beset with extremely long cilia, which move somewhat slowly. The mouth and neck of the funnel seem to be divided longitudinally by a partition. But it is probable that the partition is incomplete. (See figs. 15 and 16.) The somites of *Nereis virens* are separated by transverse mesenteries, and at the line along which these mesenteries are united to the intestine the latter is considerably dilated, while in the centre of the somite it is contracted. In order to conform to the typical nephridium in its relations, the nephrostome in *Nereis virens* ought to be on the front side of the septum, behind which the body of the nephridium is situated. Whether this is so or not I have not been able definitely to ascertain, but I believe it to be so. The septum is close to the front edge of the base of the parapodium, and the nephridium lies slanting across the entrance to the cavity of the parapodium, and above the edge of the ventral band of longitudinal muscles. Thus the distance between the septum and the body of the nephridium is not too great to be bridged by the tube leading from the nephrostome. It is to be noted that the nephridium lies as usual below the oblique muscles.

Ehlers' observation above quoted, if it were perfectly accurate, would prove beyond a doubt that the nephridia in *Nereis virens* serve to convey the sexual products, or at least the ova, to the exterior. But that observation is in contradiction to all the evidence that has come under my notice. The breeding habits of the Nereidæ still remain in some particulars mysterious, but it seems clear that the worms of

this and other errant families, becoming provided with more efficient swimming organs at the breeding season by the metamorphosis of some of their parapodia, leave their burrows and swim about freely in the water while they are discharging their reproductive elements. I have only met with two forms of the family Nereidæ in sexually mature condition—*Nereis pelagica* and *Nereis virens*. Specimens of the latter are not unfrequently thrown up on the shore in the Firth of Forth about the month of April. Solitary female specimens thus cast up have occasionally been brought to me, but I have not examined these very minutely. On May 1st this year we found about 150 specimens among the débris at high-water mark within about a quarter of a mile, close to the Granton Laboratory. Every one of these specimens proved on examination to be male; they were all alive, though some had been half desiccated by the warmth of the sun after the tide had left them, but they were not vigorous, and from their position and condition must have been dead before the tide returned. These specimens were in most cases distended with milt, and when handled they burst or broke into pieces on the least provocation and discharged the milt copiously. I cut sections of some of the nephridia of these in situ, and saw not a trace of spermatozoa within the organs. If the dehiscence is normal it seems most probable that the animals of both sexes die after discharging their sexual products, and the dehiscence is so constant that it cannot be other than a normal process. If the sexual products normally escape by dehiscence, why should they pass through the nephridia, or if they passed through the nephridia why should dehiscence occur at all?

I have not seen specimens of *Nereis pelagia* cast up by the waves upon the shore in an enfeebled condition, but we found the epitokous form of the species abundantly at the beginning of February; some we found under stones between tide marks, but the greater number among the roots of *Laminaria* and under stones in the *Laminarian* zone. We kept these often for some time in captivity, and whenever they were handled, or even without being touched, they discharged

ova and spermatozoa by dehiscence, and they invariably died after being kept some time. Sections revealed no ova or spermatozoa in the nephridia, in fact it seems impossible that the ova should be found in the lumen of the nephridium, for the ovum is many times larger than the tube of the latter in diameter, being nearly equal in size to the whole body of the nephridium.

## 2. THE "CARDIAC BODY."

Dr. R. Horst, of Leyden, in 'Zool. Anz.,' viii, published a discussion of this curious and problematic structure. He gave an account of his own examination of the heart in some specimens of the genus *Brada*, belonging to the family *Chlorhæmidæ*, and from the structure of the cardiac body in that genus, and a comparison of it with certain structures in the *Oligochæta*, draws the conclusion that the cardiac body in *Polychæta* is originally derived in the embryo from the intestinal epithelium, is, in fact, an evagination from the intestine. Dr. Horst gives a rapid sketch of the history of our knowledge of the heart in the *Chlorhæmidæ*. The organ was first mentioned by Otto in 1821,<sup>1</sup> and considered by him to be a second œsophagus. Claparède gives an erroneous description of the organ ('Ann. Chét. de Naples'); he says it is a tubular structure, which appears to open anteriorly in the dorsal wall of the buccal cavity. Delle Chiaje also considered the heart to be connected with the digestive system. Gab. Costa, Dujardin, Max Müller, and Quatrefages have all recognised the organ as a true heart, whose function is to propel the blood into the branchiæ. Claparède, however, seems to have been the first to discover the curious dark-coloured cells containing granules, which occur in the heart, while those zoologists who recognised the true function of the heart were unaware of anything peculiar in its structure. Claparède met with the cells of the cardiac body, and thought the organ was entirely glandular, while

<sup>1</sup> "De Sternaspide et Siphostomate," 'Nova Acta Acad. Caes. Leopold Nat. Cur.,' x, pars 2.



others saw that the organ was a heart, and were unaware that it contained a glandular body.

Dr. Horst found that in *Brada*, as in *Serpulidæ*, *Ammocharidæ*, &c., there is a blood sinus round the intestine, and the heart is continuous with this sinus, and therefore a true dorsal vessel, through which the blood is conducted from the walls of the intestine to the gills. It is to be remarked that this is a confirmation of the account given by Quatrefages in 'Hist. des Annelés,' 1865, i, p. 54. Max Müller, on the other hand, supposed the posterior end of the heart to be blind. Dr. Horst then points out the agreement between the arrangement described by him in *Brada* and that described by Vejdosky in the *Enchytræidæ*, which also possess a dorsal vessel only in the anterior somites, its place being supplied posteriorly by a blood-sinus in the wall of the intestine; and further says the researches of Salensky on the development of *Terebella* ('Arch. de Biologie,' t. 4) have shown that such an arrangement is in other Annelids only embryonic.

I have examined the vascular system in *Trophonia plumosa*, and although I find Horst's statements for the most part correct, there is one feature which he does not mention which might give rise to another explanation. There is, namely, a thin vessel running in the dorsal median line on the inner surface of the body wall, unaffected by the convolutions of the intestine, receiving metamerically arranged transverse vessels from the walls of the latter, and opening into the dorsal side of the heart at a point a third of its length from the hinder end (see fig. 17). It is thus a question which represents the typical dorsal vessel—this separate vessel that I have described, or the blood-sinus in the walls of the intestine. I am inclined to think the former, and that the posterior end of the heart may be taken as representing a vessel passing from the intestinal blood-sinus to the dorsal vessel, while the anterior end of the heart is the direct continuation of the dorsal vessel. These relations are shown in fig. 17.

However this may be, the thin dorsal vessel mentioned above is not represented in *Terebellidæ*, *Ampharetidæ*, and *Amphic-*

tenidæ. In those three families an anterior heart similar to that of the Chlorhæmidæ is present, and its posterior end is connected with a blood-sinus in the walls of the intestine, which is the only representative of the typical dorsal vessel. The intestinal blood-sinus is connected, on the ventral side of the intestine (e. g. in *Amphitrite Johnstoni*), with a large definite vessel, which at the level of the posterior end of the heart divides into two branches; these pass up one on each side of the œsophagus, and unite to form the heart. Thus the paradox is here true that the typical dorsal vessel is in these families chiefly represented by a ventral vessel. The usual subintestinal or ventral vessel is of course present in addition. Thus Horst's remark, that the presence of a free dorsal vessel in the anterior somites only is merely embryonic in Terebellidæ, is far from correct. Salensky, it is true, describes the arrangement as existing in the larva of *Terebella*; but he does not assert that any change occurs in later development, and, as a matter of fact, the arrangement is, as I have said, especially characteristic of the Terebellidæ, Amphictenidæ, and Ampharetidæ, in the adult condition.

But the most interesting point about this heart is the cellular body it contains. Claparède, in his 'Ann. Chét. de Naples,' mentions this body in *Terebella multisetosa*, Grube, and in *Audouinia filigera*. In describing the latter species he says there are three brown cords in the walls or in the lumen of the dorsal vessel, and similar structures are common to all the Cirratulidæ. Of the body in *Terebella multisetosa* he says that the dorsal vessel contains a substance of a deep black colour distributed in irregular cords. It is curious that Claparède should have recognised the nature of the heart in Terebellidæ, and not seen the similarity between that organ and the heart in Chlorhæmidæ. In his 'Structure des Ann. Sédentaires,' 1873, Claparède figures transverse sections of the heart of *Audouinia filigera* and of *Terebella flexuosa*, and gives a fuller account in the text of the glandular cords seen in these sections. He says that in his previous work he had supposed the cardiac organ in *Audouinia*

filigera to be formed of several longitudinal bands, but on studying sections saw that it was really a cylinder (boyau) with longitudinal folds. In *Terebella flexuosa* the brown substance forms two lobed masses, one applied to the superior part of the vessel the other to the inferior. These two masses are not independent, but united at intervals by thick connecting cords. In the brown organ of *Audouinia* the highest powers only enabled him to distinguish very fine coloured granules scattered in a fundamental mass. He thinks it possible that these brown cords are similar to the chloragogenous substance which surrounds the exterior of the ventral vessel in the Sabellidæ, remarking that in species where the cardiac body is present chloragogenous tissue is wanting, and there would thus be internal as well as external deposits of chloragogen.

Horst gives some account of the minute structure of the cardiac body in *Brada*. He describes it as made up of irregular cords, each of which has usually an oval section, and is made up of cells filled with brown granules. The limits of the cells were not always clear, and in adult specimens only a network of fibres could be seen in a section, nuclei being visible at the nodes of the network, and brown granules scattered through the ground substance of the meshes. I have examined the minute structure of the cardiac body in several species, with results slightly different to those of Horst.

(a) Fam. CHLORHÆMIDÆ.

In *Trophonia plumosa*, when the heart is examined by means of either transverse or longitudinal sections, the somewhat cylindrical cords of which the cardiac body is composed are seen not to be composed entirely of cells as described by Horst, but in most cases to be tubular, each possessing a lumen (figs. 18, 19). The cells around the lumen form a glandular-looking epithelium composed of several layers of cells; those nearest the basement membrane are solid and nucleated, and contain a large number of small, round, brown grains. The more internal cells are clear and vacuolated, and the nucleus

cannot usually be seen in them; the most internal, those nearest to the lumen, are almost spherical, and they project separately and at various levels into the lumen, just as do the similar cells in a section of a nephridium. Indeed, the whole structure recalls that of a nephridium very forcibly. Usually the lumen of the tube contains débris which is stained by carmine, and among this can be recognised spherical cells similar to those which project from the epithelium in process of disintegration. It is difficult to resist the conclusion that these tubes are glands, but I have been unable to discover any trace of an opening from the cardiac body either to the exterior of the body or into any other organ. In many of the cross sections of the cords no lumen can be seen; in some cases this is obviously due to the fact that the plane of the section is too near the surface of the cord, and has therefore passed only through the epithelium; in other cases the plane of the section is median longitudinal, or transverse, through the widest part of a cord, and yet no lumen is seen, the epithelium on one side being so thick as to come into contact with that of the other. It is probable that the obliteration of the lumen is partly due to the contraction produced by reagents. The sections of the cords in any section of the heart of *Trophonia* are small and numerous, and the whole cardiac body almost fills up the entire cavity of the heart, from its thick posterior portion to its thin anterior region; the channels left for the passage of the blood are in consequence very small. The blood contains small oval corpuscles, each showing a relatively large, well stained nucleus. These corpuscles are not numerous.

The cardiac body in *Flabelligera affinis* (*Siphonostoma*) presents a great contrast to that of *Trophonia* in its size relatively to that of the heart; in the former species the organ constitutes an irregular flat, folded band, running longitudinally through the cavity of the heart and occupying only a small portion of that cavity. Between the cardiac body and the wall of the heart is a wide space occupied by blood. The lower edge of the band is in the central line of the ventral side of the heart, whence it rises like a longitudinal partition, its upper



branched part coming into contact with the dorsal and lateral sides of the heart. The organ also differs from that of *Trophonia* in minute structure. In transverse section the band is narrow and branched; that is to say, the main band gives off other longitudinal bands of less extent than itself, so that in transverse section it appears as an irregularly branched narrow tract. No distinct lumen is visible in the centre of this tract, but there is a distinct central line which separates the epithelia of opposite sides where they come into contact. The clear vacuolated cells seen in *Trophonia* are here absent, the epithelium consisting of elongated columnar nucleated cells only; the granules are smaller and less numerous (fig. 20).

#### Fam. TEREHELLIDÆ.

In *Amphitrite Johnstoni* the cardiac body occupies nearly the whole cavity of the heart, the channels left for the passage of the blood being very small. It is composed of cylindrical cords which generally have a longitudinal direction. In prepared sections no lumen is visible in the cords, each being completely filled with a mass of cells whose outlines are somewhat indistinct, but the nuclei are large, spherical, and deeply stained. The cells are small, so that the nuclei are closely crowded together. In *Amphitrite cirrata* and *Terebella Danielsseni* the cardiac body exists, but I have not specially examined it.

In *Lanice conchilega* the cardiac body is smaller in relation to the heart than in *Amphitrite Johnstoni*. The cords are thinner, and confined to the immediate neighbourhood of the walls of the vessel, so that a large central space is left for the passage of the blood. In the cords a lumen is frequently but not always visible. The cells have a similar character to those of *Amphitrite Johnstoni* (fig. 14).

In *Terebellides Strœmi* there is but a single cord in the cardiac body, which runs longitudinally and fills up very nearly the whole cavity of the heart. In prepared sections a lumen is

visible in the centre of this cord, and the cells are so arranged as to form radii passing from the wall of the cord towards the centre.

#### Fam. CIRRATULIDÆ.

In *Cirratus cirratus* there are three longitudinal cylindrical cords occupying nearly the whole cavity of the dorsal vessel. Two of the cords occasionally anastomose and then separate again. The cells filling the cords are elongated, pale, and nucleated; the nuclei stain but the rest of the cells remains uncoloured in stained preparations. There is no lumen, and the cells are not arranged in regular radii, but are placed so that the longer axis passes from the dorsal side of the cord to the ventral. The cells contain large numbers of the usual granules, which are brown and spherical, and usually more numerous near the exterior of the cord than in the central part. In one specimen I found only two cords present of which the dorsal was the larger. The cords are quite free in the interior of the vessel, and have no connection with the walls of the latter (fig. 21).

The cardiac body is present in the families Chlorhæmidæ, Cirratulidæ, Amphictenidæ, Ampharetidæ, and Terebellidæ. The three last are closely allied, but neither of them has any other points of close agreement with either of the two first mentioned; nor are the Chlorhæmidæ and Cirratulidæ at all connected with one another. The cardiac body is present in every species belonging to the families mentioned, though it varies in details of structure in different species.

In the heart of *Polyophthalmus pictus* Edouard Meyer<sup>1</sup> has described an organ which Horst claims as the homologue of the cardiac body we have been considering. It is, of course, probable enough that Horst is right, but it must be remembered that Meyer's description is not complete enough to decide the question whether the organ in the heart of *Polyophthalmus* is similar in structure to the true cardiac body. Meyer says that a peculiar organ having the form of a thick, short tube,

<sup>1</sup> 'Arch. f. Mik. Anat.,' Bd. xxi.

which is provided with strong cellular walls, and a canal running through its axis, occurs in the cavity of the heart. The organ projects with its posterior half, at the end of which is the broad entrance opening into the axial canal, into the intestinal sinus, and is here, by means of special small muscular bundles which arise from processes round the opening, fastened on to the intestinal epithelium. The front end of the organ contains the anterior opening of the axial canal and is fastened to the anterior wall of the heart.

From this account it follows that the blood passes in at one end and out at the other of the heart organ of *Polyophtalmus*, while as yet no opening at all has been demonstrated in the cardiac body in the families above mentioned.

I have been unable to find any facts which go to support Horst's view that the cardiac body is homologous with an organ which exists in some of the *Enchytræidæ*, and which arises as an evagination from the intestine. The account given by Salensky<sup>1</sup> of the development of the cardiac body in the larva of *Terebella* is not very full, but he states that the cardiac body is at first a tube passing from the posterior extremity of the heart and terminating blindly in its interior; and this tube, from his description and figure, seems to have an opening from the exterior posterior surface of the heart. It would seem probable, therefore, that the cardiac body in *Terebella* is derived from an invagination of the wall of the heart, and not from the intestine. It is quite certain that in the adult *Trophonia* there is no connection between the cardiac body and the intestinal epithelium, closely as they come into relation. I cut a continuous and complete series of longitudinal vertical sections through the posterior part of the heart of *Trophonia*, and the intestine it rested upon, and found that there was nowhere any connection between the intestinal epithelium and that of the cardiac body.

If Horst's view were correct one would be tempted to homologise the cardiac body of *Chætopoda* with the cellular structure which grows out from the intestine and projects into

<sup>1</sup> "Études sur le Devel. des Annélides," 'Arch de Biol.' iv.

the heart in *Balanoglossus*, the structure which Bateson believes to represent the vertebrate notochord. Professor T. J. Parker<sup>1</sup> has already pointed out, in opposition to Bateson's arguments, that the vessel which lies on the same side of the intestine as the notochord in vertebrates conveys the blood from before backwards, while the dorsal vessel in *Balanoglossus* conveys the blood from behind forwards. In this respect the dorsal vessel of *Balanoglossus* agrees with the dorsal vessel of all other Invertebrata, and I am strongly of opinion that *Balanoglossus* is constructed on the same plan as a *Chætopod*. I would consider the proboscis as the præoral lobe; the nerve-cord in the collar and in the proboscis as the enlarged representative of the supracæsophageal ganglia. The circum-cæsophageal commissures are present at the posterior region of the collar, and they unite into a well-developed ventral nerve-cord. The great obstacle to this view is the presence of the dorsal nerve-cord in *Balanoglossus*. But it may be pointed out that this dorsal nerve-cord is much thinner and more insignificant than the ventral, and that the ventral is in shape and character the real continuation of the nerve-cord in the collar. The absence of nephridia and the meaning of the proboscis pore and proboscis gland are points which cannot at present be explained on the view I have advocated.

### 3. NEURAL CANALS.

The texts for the few words I have to say on this subject are two papers, one by Professor McIntosh,<sup>2</sup> published in 1877, the other by Dr. Emil Rohde,<sup>3</sup> published in 1886. The first gives a brief account of the anatomical relations of the ventral nerve-cords in the families of marine annelids, while the other discusses the giant fibres of the nerve-cord in *Aphroditidæ*. These structures are asserted by Rohde to be nerve-fibres,

<sup>1</sup> "On the Blood-vessels of *Mustelus antarcticus*," 'Phil. Trans.,' vol. clxxvii (Pt. II, 1886), p. 719.

<sup>2</sup> "Arrangement, &c., of Great Nerve-Cords in Marine Annelids," 'Proc. Roy. Soc.,' Ed., 1877.

<sup>3</sup> 'S. B. d. Königl. Preuss. Akad. d. Wiss.,' July 29th, 1886.



which commence as processes of certain colossal ganglion cells occurring in definite positions in the brain or ventral cord. He gives the following account of the giant-fibres in the genus *Sthenelais*. There are three kinds of colossal nerve-fibres: (1) some traversing the whole nervous system from the anterior to the posterior extremity; (2) some running from the posterior to the anterior extremity; (3) some starting from the nervous system on each side, and running to the periphery. He further says that if the nervous system be traced through a series of transverse sections he finds in the posterior part of the brain a colossal ganglion cell on each side which sends off a large process. This process passes first forward for some distance into the brain, then through the œsophageal commissure into the ventral cord. These two nerve-fibres unite into one which runs ventrally on one side of the ventral cord to the posterior extremity of the body. This colossal nerve-fibre is enveloped by a fibrous sheath, which is at first closely applied to it, but in its further course separates from it, and then encloses a cavity which becomes larger posteriorly, and in the middle of the body attains an enormous diameter.

Unfortunately, no figures illustrating these descriptions have yet appeared, and I have therefore had to confine myself to a comparison of my own sections with the above description. I have been totally unable to see the connections which Rohde declares to exist. I have prepared series of sections from different parts of the body of *Sigalion boa*, Johnston, which, according to McIntosh (*Invert. Fauna of St. Andrews*), belongs to Kinberg's genus *Sthenelais*. In the middle region a pair of colossal fibres, or as I shall usually call them, neural canals, appearing under a low power like tubes, are conspicuous. One of these is situated on the inner side of each cord, towards the dorsal region, and at the periphery of the cord (fig. 22). The neural canal is internal to the layer of ganglion cells, and is partially occupied by a shrunken homogeneous substance. Processes can be often seen passing off from the ganglion cells transversely, and entering the substance of the cord where they are seen to branch into fine fibrils, exactly in

the same way as that illustrated so well by F. Nansen<sup>1</sup> in his memoir on the Myzostomidæ. But I have been unable to trace any connection between the neural canal, alias giant-fibre, and a ganglion cell. Indeed, in *Sigalion* the canal or tube becomes very small long before the brain is reached, and I cannot even distinguish it in the œsophageal commissures, or in the cord immediately behind them.

In the central part of each cord in the middle region of the body are one or two tubes, which are similar in structure to the large neural canals, but much smaller.

A few words as to the character of the nerve-cords in *Sigalion* boa. The cords are nowhere separated from the epidermis. Ganglion cells are abundant beneath the ventral cords, both in the ganglia and between the successive ganglia. Above the cords is a striking development of a very peculiar tissue whose function is problematic. In the middle of the body this tissue consists of waved fibres or laminae, which are often arranged in parallel curves. These form a network whose meshes occasionally contain cells with nuclei, but usually are filled with a stained granular substance. Close behind the head this mass of tissue is of very great size, and is much more cellular. In the œsophageal cords it is reduced to a very small quantity, but it forms a thick envelope round the brain. The tissue stains with difficulty. It is in all probability a kind of connective tissue not directly concerned in nervous functions.

With regard to *Aphrodite*, I entirely agree with Rohde that colossal fibres or neural canals are altogether absent; and in this genus the nerve-cords are quite separated from the epidermis.

*Polynœ* I have not examined, but in *Harmothœ imbricata* I find a pair of neural canals corresponding in position to those of *Sigalion* boa, but I have not seen any in a ventral position, such as those mentioned by Rohde in *Polynœ*. In *Harmothœ* the ventral nervous mass is distinctly defined, but not separated, from the epidermis.

<sup>1</sup> 'Bidrag til Myzostomernes Anatomi und Histologi,' Bergen, 1885.

Of the Nereidæ I have examined *Nereis virens*, Sars, and here cannot confirm the account of the neural canals given by McIntosh. In many sections three or four neural canals are seen, which are not quite symmetrical; these are sections through inter-ganglionic transverse commissures. In the cords between successive ganglia there are seen to be a single pair of canals, one of which is often divided into two. The pair occupy an exactly similar position to that of the neural canals in *Sigalion*. McIntosh states that in *Nereis virens* there are several neural canals, viz. two large infero-lateral, a single superior median and a smaller, a little below the latter on each side. This apparently means five in all, two pairs and one median. Probably he examined sections of the ganglia in which several canals are often seen. But these have not a constant relative position, and are, I believe, due to the subdivision of the two canals which are seen in the separated cords.

In *Nereis pelagica* I find canals placed in the positions ascribed by McIntosh to those of *N. virens*. There is one dorsal median in the fibrous partition between the cords, a pair corresponding to the typical pair of *Sigalion*, and another pair consisting of one on the external border of each cord.

In *Nephtys*, instead of the typical canal on the inner side of each cord, there are two large canals, one above the other, with a smaller one between them. There is also a smaller canal in the external side of each cord, and still smaller ones in the substance of the cords. The nerve area here is not separated from the epidermis.

In *Phyllodoce* no well-marked neural canals can be distinguished. The cords are widely separated from the epidermis.

We pass now to the examination of the families of *Sedentaria*.

In the *Sabellidæ* there is a pair of canals or tubes of much greater size than any seen in the *Aphroditidæ*. Only a few somites behind the head these tubes reach a thickness equal to or even slightly greater than that of the nerve-cords themselves, and they retain an almost uniform thickness in their course to

the end of the body. These tubular fibres have been well described by Claparède<sup>1</sup> as they occur in *Spirographis Spallanzanii*. He found several transverse connecting branches between the two tubes in the thoracic region immediately behind the union of the œsophageal commissures, and he traced the tubes into these commissures, where each divided into two branches. These branches passed forwards into the cerebral ganglion, where they ramified into thinner and thinner branches, but the ultimate terminations Claparède could not discover.

I have endeavoured to trace the anterior extremities of the tubes in *Sabella penicillus*. I found a transverse connecting tube in the first transverse commissure, like those described by Claparède, but could not find more than one, and it is noticeable that while Claparède mentions a number of these anastomoses in the text he figures only one. I found that the tube, much diminished in diameter, passed up the œsophageal commissure, but could not discover that it branched. In my sections it seems to become smaller and smaller, and simply end blindly.

In *Sabella* the mass of ganglion cells representing the cerebral ganglion is situated on each side of the œsophagus, and below it is the fibrous œsophageal commissure, which is continued by an arch above the œsophagus into its fellow of the opposite side. The tubular fibre ends below this mass of cerebral ganglion cells, and, as far as I can see, sends no branches towards the mass, nor could I see any trace of a connection between the end of the tube and any ganglion cells.

Although these structures are spoken of as tubes, they are not actually empty. Their interior in the sections is partially filled by a transparent gelatinous-looking mass, which for the most part does not stain; but there are lines in the mass which are stained, and which somewhat resemble a network of fibres. In my opinion these stained lines are due to the unequal coagulation of the gelatinous mass, which during

<sup>1</sup> "Structure des Annélides Sédentaires," 'Mém. Soc. de Phys. de Genève,' tom. xxii.



life is homogeneous and semi-liquid. On the dorsal side of the tube is a space between the gelatinous medulla and the wall of the tube, and the edge of the medulla below this space is deeply stained. All this is, in my opinion, the consequence of contraction and coagulation.

*Myxicola* in the greater part of its body has a single tubular fibre similar in structure to one of the pair which exist in *Sabella*. According to Claparède (loc. cit.) the tubular fibre of one side, at a point a little behind the œsophageal commissures, opens into that of the other side, and the latter proceeds as the unique fibre, while the nerve-cord corresponding to the first tube joins the other cord without fusing with it and finally terminates. My series of sections of this animal is not quite perfect, but, as far as I can judge, Claparède has been somewhat deceived. It is true that only one tubular fibre persists, but it seems to me that the other terminates and does not open into its fellow. Some distance behind the œsophageal ring the right hand cord is seen thicker than the other and destitute of a tubular fibre; the tubular fibre is seen on the left-hand side of the ventral median mesentery, which is pushed considerably to the right. Farther back the tubular fibre becomes central, and the two nerve-cords, one on either side of it, are equal in thickness. I have seen no indication of the disappearance of one nerve-cord. In my opinion, all that has happened in *Myxicola* is that one of the large tubes has disappeared except in the extreme anterior region, and the other has increased in size, and in the greater part of the body become central. One very interesting point to be seen in *Myxicola* is that the two tubes are continuous with one another in the lower part of the cerebral commissure; the tubes in each œsophageal commissure, which are of considerable diameter, can be seen to become continuous with one another in the section of the cerebral commissure. In my sections of *Myxicola* the tube in the posterior part of the body is entirely empty, except in the ventral part, where a thick stained band occupies the cavity; this is due to a greater shrinking of the contents of the tube in the process of prepa-

ration. It may be pointed out here that the nerve-cords in *Sabella* are not separated from the epidermis, while in *Myxicola* they are completely so.

We pass now to consider another family in which colossal tubes or neural canals are greatly developed, the *Spionidæ*. In *Nerine coniocephala*, Johnston (fig. 23), the nerve-cords are differentiations in a thickened epidermis, less distinctly defined from the surrounding cells than is the case in *Sabella*. In the median line between the two cords is an enormous neural canal, larger in sectional area than the two nerve-cords together, but having a structure similar to the tubes in *Sabella*. The appearance of this canal in section is seen in fig. 23. The canal contains a shrunken, gelatinous-looking mass as, in other cases. On tracing this canal forwards it is found to become smaller near the anterior end, and to cease altogether much sooner than is usually the case. I have found no indication of its anterior division into two canals. The last trace of it seen in approaching the head is shown in fig. 24.

In *Scolecopsis vulgaris*, Malmgren, there are two neural canals, one on the inner side of each nerve-cord.

In *Magelona*, which forms a family by itself, there is a very large median neural canal resembling that of *Nerine*, but lying below the nerve-cords instead of above them (fig. 25).

In the *Ariciidæ* I need only confirm the account given by McIntosh, that in the middle of the body the nerve-cords are thrust inwards by the great ventral longitudinal muscles, which contain between them a narrow lamina preserving the connection between the nerve-cords and the epidermis. A single median neural canal runs above the nerve-cords as in *Nerine*.

In *Arenicola* (*Telethusidæ*) the nerve-cords are separated from the epidermis by the layer of circular muscles; there is a small neural canal, entirely filled with a homogeneous mass, at the dorsal and inner side of each cord.

In *Trophonia* (*Chlorhæmidæ*) McIntosh does not mention the existence of neural canals, but one of these exists in each

cord on its inner side dorsally. The cords are entirely free from the epidermis. The neural canals are similar in size and appearance to those in *Sigalion* *boa*.

Among the *Terebellidæ* I find a median neural canal in *Lanice conchilega*, Malmgren: it is of considerable size, but has not such well-defined fibrous walls as are usually present. In *Amphitrite Johnstoni* I have been unable to detect any canal, nor in *Terebellides Strœmi*.

In the *Ampharetidæ*, however, which are, so to speak, on the way towards the *Terebellidæ*, the neural canals are large and conspicuous, and have the typical structure. In *Melinna cristata* there is one on the inner side of each nerve-cord in the thoracic region.

In the *Capitellidæ* (*Capitella* and *Notomastus*) the nerve-cords lie in the epidermis posteriorly, while in a few of the anterior somites they are entirely separated from it by both the circular and longitudinal muscles. In this anterior region there is a large median neural canal on the dorsal side of the double cord in *Notomastus*. In *Capitella* the canal is absent.

Among the *Maldanidæ* I have examined *Nicomache lumbricalis* and *Axiothea catenata*. In the former the nerve-cords are not separated from the epidermis, and there is a considerable single median neural canal above the cords in both species.

Among the *Hermellidæ*, in *Sabellaria*, as pointed out by McIntosh, the two cords are at a considerable distance from one another; they are completely separated from the epidermis and lie on the upper and inner side of the ventral longitudinal muscles. Each has a large neural canal, similar to that of *Sabella*, on its inner side (fig. 26).

In *Serpula* the neural canals are similar in structure and position to those of *Sabella*.

McIntosh mentions a small and indistinct neural canal in *Ammotrypane aulogaster*, H. R. In some of my sections it can be made out, but always with difficulty, as it is exceedingly ill-defined. In *Cirratulus cirratus*, also, neural canals are absent.

It would be very startling, if not even absurd, to maintain that such neural canals as are seen in *Sabella*, and in *Nerine* are colossal nerve-fibres, and that their contents form a nervous medulla which commences as a process from a ganglion cell. I have entirely failed to trace any connection between these canals and any ganglion cells. At the same time it is difficult to refuse to admit that the neural canals of the *Sedentaria* are completely homologous with those of the *Errantia*.

In my opinion, in both cases they are supporting structures which serve to prevent the nerve-cords being bent at a sharp angle, causing them always to remain in curves, and so to escape injury during the wriggling and burrowing of the worm. It is noticeable as a support of this view that the canals always reach their greatest development in worms which are extremely long in proportion to their thickness. *Sabella* and *Nerine* are both extremely long, as compared, for instance, to *Ophelia* or *Cirratulus*. Another fact, which seems to have some significance, is that where the neural canals show their maximum development the nerve-cord is not separated from the epidermis, and is therefore more exposed to the danger of being injured than where they have reached a more internal position. The origin of the vertebrate notochord from the hypoblast seems so well established that a comparison of it with the neural canals of the *Chætopoda* will scarcely be regarded seriously by morphologists. At the same time, seeing that the notochord at a later stage is separated from the intestine by the aorta, it is very difficult to understand how the former structure could have been derived phylogenetically from the intestine. The neural canals are remarkably constant throughout the *Chætopoda*, those in the *Polychæta* being obviously homologous with the three giant-fibres in the earthworm and other *Oligochæta*. They have a position in relation to the nerve-cords and ventral blood-vessel which is similar to that of the notochord in relation to the neurochord and aorta. Their origin in the embryo has not so far as I know been investigated, so that it is doubtful whether they are intercellular or intracellular in origin. I hope to devote further attention to



the subject, at present I can only say that the evidence adduced in favour of their specifically nervous nature is quite inadequate, and that the possibility of a phylogenetic connection between these neural canals in the Chætopoda and the notochord of the Chordata, cannot at present be altogether dismissed.

In concluding this paper I have to explain that my attention was attracted to the points discussed in the course of a systematic examination of the Polychæta, which I carried on at the Granton Marine Station, in collaboration with my friend Mr. G. A. Ramage, Vans Dunlop Scholar in Edinburgh University.

For the facts and views I have set forth I am alone responsible, but the collection and identification of specimens were chiefly carried on by Mr. Ramage, and he rendered much valuable assistance in preparation and dissection. The drawings for the paper were all executed by myself.

## EXPLANATION OF PLATES XVII, XVIII, and XIX.

Illustrating J. T. Cunningham's paper "On Some Points in the Anatomy of Polychæta."

FIG. 1.—An entire nephridium of *Arenicola marina*, seen under a low power, in the fresh state. The membranous funnel has been turned back, so that the ventral side is seen. *A.* Anterior, *P.* Posterior end. *bl.* Blood-vessel, which joins the branchial vein. *d. b.* Dorsal fringed border of nephrostome. *ne.* Nephrostome. *go.* Gonad.

FIG. 2.—Optical section of a portion of the wall of the nephridium of *Arenicola*, after treatment with osmic acid. *bl.* Blood-vessel. E, Zeiss, oc. 3.

FIG. 3.—Horizontal section of 2nd and 3rd and part of 1st somites of *Cirratulus cirratus*. *ne.* Nephrostome of anterior nephridium, opening from buccal somite. *a. n.* Ascending part of the nephridium. *d. n.* Descending part. *se.* Transverse and longitudinal septa. A, Zeiss, oc. 2.

FIG. 4.—Horizontal section through three somites, from middle part of body of the same species. *ne.*, *se.*, as before. An ovum is seen in one of the nephrostomata. A, Zeiss, oc. 2.

FIG. 5.—Transverse section of same species, middle part of body, passing through external openings of a pair of nephridia. A, Zeiss, oc. 2.

FIG. 6.—Two somites of *Cirratulus cirratus*, seen living by reflected light while the eggs were escaping. In one somite an ovum is shown just emerging from the nephridial aperture.

FIG. 7.—Portions of two consecutive somites, from a vertical longitudinal section of *Nerine cirratulus*. *ne.* Nephrostome. *ov.* Ovary. *no.* Notopodial chætæ. *nu.* Neuropodial chætæ.

FIG. 8.—Portion of a section of the same series as the preceding, nearer the surface of the body. *no.*, *nu.*, as before. *np.* External opening of the nephridium.

FIG. 9.—Longitudinal vertical section of *Nerine coniocephala*, showing relations of the nephridium. Reference letters as before.

FIG. 10.—Fresh preparation made by cutting open the anterior part of a specimen of *Lanice conchilega* along the dorsal median line, taking away the intestine and cutting through the oblique muscles on each side. *n.* Nephridia, with looped tubes. *n'.* Reduced nephridia. *n. r.* Rudimentary nephridium of 5th somite. *no.* Notopodial chætæ, their inner ends.

FIG. 11.—Horizontal section of anterior nine somites of *Lanice conchilega*, at a level near upper end of the uncinigerous tori. *n.* Continuous tube formed by nephridia of Somites VI to IX. *n. a.* Ascending part of nephridial tube. *n. p.* Nephridial aperture. *v. gl.* Tissue of ventral glandular epidermis.

FIG. 12.—Similar horizontal section of Somites XI to XIV. *n'.* Coalesced reduced nephridia. *nu.* Neuropodium, *i. e.* uncinigerous torus.

FIG. 13.—Horizontal section of somites II to V of *Lanice conchilega*, from the same series as that shown in Fig. 11. *ne.*, *ne.*, *ne.* Nephrostomata of Somites II, III, and IV, with gonads attached to the posterior two. *n.* Section of nephridial tube in Somite III.

FIG. 14.—Transverse section of *Lanice conchilega* in Somite X. *n'.* Cavity of reduced nephridium. *d. b.* Dorsal blood-vessel. *v. gl.* Ventral glandular epidermis.

FIG. 15.—Nephridium of *Nereis virens*, as seen in fresh state, when dissected out from the animal. *ne.* Nephrostome with its fringe of branched ciliated processes. *n.* Globular mass, formed by the convoluted nephridial tube. *n. p.* Cylindrical portion leading to external aperture. A, Zeiss, oc. 2.

FIG. 16.—Nephrostome of *Nereis virens*, more highly magnified; fresh condition. Zeiss, C C, oc. 3.

FIG. 17.—Pseudhæmal system of *Trophonia plumosa*, as seen on dissection. *d. v.* Dorsal vessel. *v. v.* Ventral vessel. *ht.* Heart. *int.* Intestine. *o. p.* Subœsophageal pouch. *ov.* Ovary.

FIG. 18.—Vertical longitudinal section through the heart and adjacent part of the intestine of *Trophonia plumosa*. *bl.* Blood or pseudhæmal fluid. *c. b.* Tubes of the cardiac body; some with an open lumen, others full of transparent cells. *ep.* Epithelium of the intestine. A, Zeiss, oc. 2.

FIG. 19.—A single tube of the cardiac body shown in previous figure, more highly magnified. Shows the nucleated cells lining the wall and a large central lumen. E, Zeiss, oc. 2.

FIG. 20.—Transverse section of heart of *Flabelligera affinis*, showing cardiac body in the interior. A, Zeiss, oc. 2.

FIG. 21.—Transverse section of dorsal vessel and contained cardiac body in *Cirratus cirratus*. *c. b.*, *bl.*, as before. E, Zeiss, oc. 2.

FIG. 22.—Transverse section of ventral nerve-cords of *Sigalion* boa, from middle of body, interganglionic region. *n. co.* Nerve cord. *n. c.* Neural canal. *s. n.* Supraneural connective tissue. *ed.* Epidermis. *ct.* Cuticle.

FIG. 23.—Transverse section of nerve-cords of *Nerine coniocephala*. *n. co.*, *n. c.*, as before.

FIG. 24.—Transverse section from same series as preceding figure, near the anterior end of the animal. Letters as before. C C, Zeiss, oc. 3.

FIG. 25.—Transverse section of *Magelona papillicornis*. *n. c.*, as before.

FIG. 26.—Transverse section of *Sabellaria spinulosa*, middle of the body. *n. co.* Nerve cord, with its neural canal.

## On Temnocephala, an Aberrant Monogenetic Trematode.

By

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With Plates XX, XXI, and XII.  
X  
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### HISTORICAL.

ABOUT the year 1849 Gay discovered, in the environs of Santiago, on the surface of certain crayfishes, a leech-like animal, which, in a letter to Blainville, he described briefly under the name of *Branchiobdella chilensis*.<sup>1</sup> The genus *Branchiobdella* was first instituted by Odier, and, though apparently the name was applied by him to a species of the genus *Branchellion* of Savigny, it has been very generally adopted since for an external parasite of the fresh-water crayfish of Europe—the *Branchiobdella astaci* of Rudolphi.

*Branchiobdella astaci*, as is well known, is a well-marked Leech; it has an elongated body composed of about eighteen distinct rings, with an anterior and a posterior sucker, an anal aperture above the posterior sucker, and a median ventral nerve-cord. In Gay's 'Zoology of Chilé,'<sup>2</sup> Blanchard described Gay's species under the name of *Temnocephala chilensis*, recognising that the differences between it and *Branchiobdella astaci* are too great to admit of both species being placed in one genus. "Las Temnocefalas se distinguen aun

<sup>1</sup> I am not aware that the letter has been published, but it is quoted by Moquin-Tandon in the 'Monographie des Hirudinés,' p. 300.

<sup>2</sup> ii, p. 51.



del género *Branchiobdella* por la presencia de los ojos y de las divisiones cefálicas de que no existe traza alguna en él.”

In 1870, Philippi<sup>1</sup> published some observations on *Temnocephala*, based on an examination of living specimens which he found on the surface of Chilian fresh-water crayfishes of the genus *Æglea*. He described the external form, the colouration, and the movements, and notices certain of the internal organs which he is able to see through the wall of the body, though without being able to give any precise account of their nature. He concludes that *Temnocephala* ought to be placed among the worms in the neighbourhood of *Malacobdella*.

During his scientific explorations in the Phillipine Islands, Carl Semper found, on the surface of fresh-water crabs, specimens of an external parasite, which proved to be the *Temnocephala* of Blanchard; but a more detailed examination showed him that the affinities of the animal were much more with the ectoparasitic Trematodes than with *Malacobdella* or the Hirudinea.<sup>2</sup>

Wood-Mason found, in 1875, a number of *Temnocephalæ* in a bottle containing some New Zealand crayfishes (*Paraneuphrops setosus*), to which they had evidently been attached, and some also in bottles containing specimens from the north-east frontier of India.<sup>3</sup>

At the beginning of last year, when on a visit to Tasmania, my attention was directed by Mr. Alexander Morton, the curator of the Tasmanian Museum at Hobart, to certain remarkable animals observable on the surface of a specimen of the large fresh-water crayfish of the northern waters of Tasmania, which he had alive in a tank. These proved to be

<sup>1</sup> ‘Archiv für Naturgeschichte,’ 1870.

<sup>2</sup> ‘Zeitschrift f. wiss. Zoologie,’ xxii Band (1872). I have not been able to see this paper, which is a very short one (three pages), and am indebted for my knowledge of it to Leuckart’s “Bericht” in the ‘Archiv f. Naturgeschichte,’ xl Band (1874).

<sup>3</sup> “On the Geographical Distribution of the *Temnocephala chilensis* of Blanchard,” ‘Ann. Mag. Nat. Hist.’ (4), vol. xv, p. 336 (1875).

Temnocephalæ; and I have since found that other species of this remarkable genus infest the fresh-water crayfishes of the rivers of New South Wales.

I must here acknowledge my indebtedness to various friends, through whose kindness I have been able to procure ample supplies of specimens, more especially to Mr. Alexander Morton, of Hobart; Mr. E. C. Merewether, and Mr. Harry Merewether, of Bondi and Mount Wilson; Mr. Alexander Hamilton, of Mudgee; Mr. J. D. Cox, of Mount Wilson; Mr. Charles Chilton, of Dunedin, and Mr. J. J. Fletcher.

#### GENERAL DESCRIPTION OF TEMNOCEPHALA.

Temnocephala (Pl. XX, figs. 1—5) is a leech-like animal, the largest about half an inch in length. In outline the body is ovate or pyriform, but much compressed from above downwards; the anterior end narrower than the posterior, and the lateral border fringed with a narrow, delicate fold. At the narrower anterior end there is, in the middle, in the case of the Tasmanian species, a rounded, dorso-ventrally compressed lobe, about a fifth of the length of the rest of the body, and on either side of this two very long and slender tentacles, which are filiform, and a half to two thirds of the total length of the body when fully extended, but are capable of being greatly retracted. In the case of the New South Wales species, and that from New Zealand, there are five equal slender tentacles. Close to the broader posterior end on the ventral aspect is a very large sucker of circular outline supported on a short stalk. Near the middle line of the dorsal surface, placed near together a little behind the bases of the tentacles, is a pair of small black eyes. On the ventral surface, not far from the anterior end, is the mouth—a well-marked aperture. Some distance behind it, a little way in front of the sucker, is the common genital aperture—a short transverse slit leading into the genital cloaca.

By incident light against a dark ground, the body of the larger New South Wales species (fig. 2) and of the Tasmanian

species (fig. 3) has a dark grey ground colour with rich brown mottling. In the New South Wales species there are several, usually three, broad transverse dark bands, separated from one another by lighter intervals. In the middle of the most anterior of these, towards its front edge, about a fifth of the total length behind the base of the tentacles, is the dark spot on which the eyes are situated, and in front of this is a lighter interval, succeeded in front again by a dark space about the bases of the tentacles; the latter are of a nearly uniform brown, rather lighter towards the tips. Slightly behind the eyes, and rather nearer the lateral margin than the middle line, there will be seen on either side a minute white spot, which marks the position of the opening of the excretory system.

Little is to be seen of the internal organisation on a surface view, the pigment of the integument being very dense. A few light reticulating lines may be observed, which indicate the position of the elements of the dorsal nerve-plexus, the alimentary canal may be discerned as a lighter patch of squarish outline towards the middle of the body, and a few, irregularly-placed, fine transverse lines may be observed, which marks the position of rudimentary intersegmental septa.

On the ventral side the colour is light grey; the sucker is colourless. The squarish intestine, of a darker colour, is seen through the body wall, and transverse divisions of its substance indicate the intestinal pouches or cæca.

Here and there among the full-grown *Temnocephalæ*, in the case of the larger New South Wales species, will be found smaller immature specimens, distinguished by their whiteness; and when these are examined under the compressorium a good deal is to be learnt regarding the internal organisation. They are almost entirely devoid of pigment, except a little in the neighbourhood of the eyes and along the back, and, strange to say, they have invariably six tentacles, whereas the adult has only five.

When undisturbed the *Temnocephalæ* adhere to the surface of the crayfish by means of the sucker, with the body extended and inclined at an angle of about  $45^{\circ}$  to the surface

of attachment, the long slender tentacles stretched to their utmost and waving about the water in search of food. Their food consists of small crustacea (small Amphipoda in the case of the New Zealand species, small Aselli and Entomostracans in the case of the New South Wales species) and insect larvæ. These they capture by means of the tentacles, and it is readily to be understood that living on the crayfish must be of advantage to the animal, the movements of the crayfish in searching for food amongst the stones and dead leaves and sticks on the bottom of the stream doubtless starting many of these Arthropods, and enabling the Trematodes to secure them.

The *Temnocephalæ* move from place to place with a sort of "looping" action very like the movements of a leech. The body is applied to the surface of the crayfish and then stretched out; the tentacles become shortened and flattened out on the surface of the crayfish and play the part of anterior suckers; the large sucker is relaxed and the body drawn forwards by means of the tentacles, until the sucker is fixed again close up to the latter, the body being now bent double; the tentacles then let go their hold, the body is stretched out again and so on. The body can be rotated from side to side through a very large arc by the action of the sucker, which is capable of a considerable amount of rotation around its short stalk. The rapidity of all these movements and the extreme sensitiveness of the animals are surprising. A slight touch from an instrument will cause an instantaneous turning aside of the body, drawing in of the tentacles, and frequently rapid flight in a different direction from that in which the attack was made. In turning aside from a touch the little animals show a very definite sense of direction, and if a succession of taps be made on the bottom of a vessel in which they are living, alternately on opposite sides of them, they will turn from one side to the other according to the direction of the tap. If they are detached from the surface of the crayfish—which it is very difficult to do owing to the slippery character of their integument and the firmness with which the sucker adheres—they contract themselves for a moment into a ball, then stretch-



ing themselves out to their full length and extending their tentacles, they are often able by strong flexions of the body while falling through the water to seize on some other part of the surface and regain their position on the crayfish. The movements thus made in the attempt to regain a hold are not unlike the movements made by the leech when swimming, but the *Temnocephalæ* are incapable of directed movement or even of sustaining themselves in the water by this means. When the body is pinched or cut, the tentacles are very often turned backwards and clasp the instrument used as if to ascertain its nature or to repel the attack, and the tentacles are to be regarded as special organs of touch as well as instruments of prehension and aids to locomotion.

Four very distinct species of *Temnocephala* frequent the Australian and New Zealand crayfishes, and all of them, so far as I am able to judge from Philippi's figures, differ from *T. chilensis*. That found on the surface of the larger Tasmanian crayfish is distinguished by the possession of a short compressed lobe instead of the median tentacle. All the others have, like *T. chilensis*, five equal or nearly equal tentacles; but are to be distinguished from one another by certain differences in the structure of the reproductive organs to be noticed later on. I propose the following names for the four species:

1. *TEMNOCEPHALA FASCIATA*, on *Astacopsis serratus*, streams of New South Wales.

2. *T. QUADRICORNIS*, on *Astacopsis Franklinii*, northern rivers of Tasmania.

3. *T. MINOR*, on *Astacopsis bicarinatus*, streams of New South Wales.

4. *T. NOVÆ-ZELANDIÆ*, on *Paranephrops setosus*, rivers of New Zealand.

#### INTEGUMENT, MUSCLES, AND PARENCHYMA.

The body wall is composed of the following layers—cuticle, epidermis, basement membrane, circularly arranged layers

of muscular fibres, longitudinal layer of muscle, nervous layer.

The cuticle (Plate XXI, fig. 1, *c.*) attains a thickness of  $\cdot 006$  mm. in *T. fasciata*. It is beset with numerous vertical pore-canals, the presence of which gives it the appearance in sections of being made up of close-set papillæ. On a surface view it appears slightly corrugated, the rugæ being exceedingly minute, irregular, and mostly transverse.

The epidermis (*e*) is of nearly equal thickness with the cuticle. It is composed of a thin layer of protoplasm, with regularly distributed nuclei, but without a trace of cell-boundaries. The nuclei are spherical, of a diameter nearly equal to the whole thickness of the epidermal layer, and with a finely granular interior. In vertical section the substance of the epidermal layer appears to be divided into a series of vertical columns by a number of parallel lines. This appearance is produced by the presence of very numerous pore-canals, which run perpendicularly through both epidermis and cuticle to open on the surface of the latter; and a surface view of the epidermis shows the numerous and closely-placed rounded openings. In *T. minor* the cuticle is smooth, and the nuclei in the epidermis much less numerous than in *T. fasciata*.

The basement membrane (*b.*) on which the epidermis rests is a perfectly homogeneous membrane of, comparatively, considerable thickness, being as thick as the epidermis itself. It stains deeply with carmine dyes—much more deeply than the epidermis, but is not readily stained with hæmatoxylin. It is devoid of nuclei or other evidence of structure; like the superficial layers it is perforated by the pore-canals, but it is difficult to see them unless in parts where the secretion of the subcutaneous glands, which is readily acted on by staining agents, is passing out. Like the cuticle and epidermis the basement membrane varies little in thickness in different parts of the body. In *T. minor* cuticle, epidermis, and basement membrane are very delicate, and together are only  $\cdot 008$  mm. in thickness.

The external muscular layer (*c. m.*) is a thin stratum of circularly arranged fibres, not more than one or two fibres in thickness. It is situated in a stratum of finely fibrous matter containing a layer of pigment cells, which in *T. fasciatus* on the dorsal side form with their anastomosing processes a dense and regular network; this pigment-bearing stratum is much more strongly developed on the dorsal side than on the ventral.

The internal layer of muscle (*l. m.*), the fibres of which run longitudinally, is much more strongly developed than the external layer, and is composed of thicker fibres; it is most powerfully developed on the ventral side, but extends over the whole surface and is specially well developed in the tentacles on the ventral side. The fibres on the dorsal side are arranged in bundles, separated from one another by very narrow interspaces occupied by interstitial fibrous matter containing pigment; on the ventral side they are arranged in thin fasciculi.

The muscular fibres of these two layers are usually angular, sometimes oval in cross section, .004 mm. in diameter in the internal layer, rather less in the external. They are finely striated longitudinally, non-nucleated, and are separated from one another by finely fibrillar interstitial matter. In cross section they are seen to consist of two substances, one forming a narrow darker central core, the other clearer and constituting the principal bulk of the fibre.

The nervous layer is a thin layer of the parenchyma, distinguished by the presence in it of a considerable amount of pigment, and by being the seat of the superficial nerve-plexuses. It passes insensibly into the general parenchyma of the centre of the body.

In the structure of the body wall *Temnocephala* resembles the marine ectoparasitic Trematodes such as *Tristomum* and *Onchocotyle*, and differs essentially from the Distomidæ in the presence of the pore-canals and the absence of distinct cell-boundaries in the epidermis; the inner cell-layer described by Sommer<sup>1</sup> in the liver-fluke is not represented,

<sup>1</sup> "Die Anatomie des Leberegels," 'Zeitschr. f. wiss. Zool.,' xxxiv Band.

but its existence in the latter species has been denied by Mace.<sup>1</sup> The layer of oblique muscular fibres found in the body wall of some Polystomidæ, though absent in others, is not here represented.

The interstices between the various organs and the wall of the body are occupied by the parenchyma, which consists of a variety of areolar fibrous tissue with very delicate anastomosing fibres with plates and nuclei. In the interspaces of this network are occasionally cells which having no distinctive character may be called parenchyma cells; but these only occur irregularly and are entirely absent in many places. To be regarded perhaps as modified cells of the parenchyma is a layer of very large cells (Pl. XXI, figs. 3 and 4) lying between the longitudinal layer of muscle of the body wall and the testes, and extending from the region of the pharynx in front to that of the genital aperture behind. These are the subcutaneous gland-cells whose function is the secretion of slimy and viscid matter to be discharged on certain areas of the outer surface. The fibrous tissue of the parenchyma forms wide meshes in which these cells are contained. The cells themselves are of colossal size, averaging .066 mm. in diameter, with a large vesicular nucleus like that of an ovum, and a spherical solid-looking nucleolus. The substances of the protoplasm of these cells presents three principal modifications. In the first of these forms there is only a very delicate protoplasmic network in which the threads have a tendency to radiate outwards from the nucleus to the periphery. In a second form there occur in the interstices of the network a greater or smaller number of rounded granules, .004 mm. in diameter. In the third variety the place of the network is more or less completely taken up by numbers of bacilliform bodies, about .02 mm. in length, slender, and with a slight enlargement at one end. Intermediate stages between the two last forms are also to be observed, the contents of the cell consisting of oval bodies, each of which is enclosed in a clear

<sup>1</sup> "Recherches anatomiques sur la grande douve du foie (*Distoma hepaticum*)."[Abstract in 'Zool. Jahresb.,' 1882, i, pp. 230, 231.]



spherical space. The secretions of these cells have two distinct destinations. In the case of the more posterior cells of the gland (Pl. XXI, fig. 2, *d.*) the secretion passes out of the cell by a narrow elongated neck or duct without well-defined walls, and reaches the exterior by perforating the muscular layers and passing through basement membrane, epidermis, and cuticle by means of the delicate pore-canals. The numerous "ducts" of these cells, which branch and anastomose in their course, pour their secretion over a considerable area of the ventral surface in front of and behind the genital aperture, and all over the ventral surface of the sucker. The function of these cells which discharge around the genital opening is, doubtless, the secretion of the viscid matter by means of which the eggs adhere together, while that of the cells discharging on the sucker is the formation of a similar sticky secretion adding to the adhesive power of the organ. The most anteriorly placed of the cells discharge their contents into a system of narrow anastomosing channels which run between them. These channels unite on each side anteriorly to form a larger duct which runs forwards into the region of the head, past the excretory sac, and breaks up in front into branches which open on the exterior (through the pore-canals) on the ventral aspect of the tentacles. The secretion here voided is a viscid matter similar to the secretion of the posterior part of the gland, and its function is obviously to add to the prehensile power of the tentacles.

Scarcely to be distinguished from those subcutaneous unicellular glands are certain gland-cells at the base of the penis, secreting a substance containing spherical granules which reaches the interior of the ejaculatory duct to become mingled with the testicular secretion; but, though apparently merely a part of the subcutaneous system of unicellular glands, this group of cells on account of the special destination of its secretion is best considered along with the reproductive organs.

The system of muscular fibres of the parenchyma is highly developed. In general they occur either singly or in narrow bands, running (Pl. XXII, fig. 17, *d. v. m.*) either trans-

versely or obliquely through the parenchyma from the dorsal to the ventral aspect, and inserted at their extremities into the basement membrane. In the region of the intestine, however, the muscular fibres of the parenchyma form a series of about twelve incomplete transverse dissepiments (Pl. XXI, fig. 8, *sept.*), constricting the intestine at regular intervals, and dividing the peri-intestinal region into a series of incompletely separated segments. Continuous with these are the layers of muscular fibres investing the alimentary canal and the reproductive organs.

The muscular fibres of the sucker are derived both from the muscle of the body wall and from that of the parenchyma. There are six sets of fibres to be distinguished, viz. (1) fibres which pass from the dorsal wall of the body to near the centre of the concavity of the sucker; (2) oblique fibres which run through the substance of the outer part of the sucker from the dorsal to the ventral surface; (3) fibres which run longitudinally from the ventral body wall obliquely through the lateral parts of the stalk; (4) radial fibres; (5) circular fibres running round the margin; (6) accessory fibres.

#### ALIMENTARY CANAL.

The mouth is situated on the ventral surface, near the anterior end of the body, rather behind the plane of the eyes and the excretory openings. It is a transverse opening of considerable width, leading directly into the cavity of the muscular pharynx. The latter is a subspherical organ with thick walls and a relatively small cavity. The wall of the organ (Plate XXI, fig. 6) is constituted as follows. Most internally is a thick membrane (*ep.*), almost homogeneous in character, but very finely granular, and very finely striated in a vertical direction. The substance of which this membrane is composed is not cuticular, but, though entirely devoid of nuclei, is to be taken as the equivalent of an internal epithelium. Running right through the substance of the wall of the pharynx is a series of radially arranged muscular fibres (*rad.*);

each of those divides both externally and internally into two or three parts ; internally, these pass into the internal layer, in which they are traceable for a little distance as vertical lines ; externally, they are affixed to the most external layer. Between the radiating fibres, which are not closely placed, is a finely fibrous material, which is little acted on by staining agents, and embedded in this, here and there, is a large ganglion-cell. Besides these radiating fibres the wall of the organ comprises four layers of circularly arranged fibres ; the most internal layer (*i. c. l.*) is longitudinal in direction, the second and third (*e. c. t.* and *i. c. t.*) transverse, and the fourth (most external *e. c. l.*) longitudinal.

The intestine (Plate XXI, fig. 5) is a wide, dorso-ventrally compressed sac of rectangular outline, nearly as broad as long, which occupies about the middle third of the length of the body and more than half its breadth. It is surrounded on all sides, and to some extent also in front and behind, by the rounded lobes of the vitelline glands ; in the middle in front it comes into relation with the pharynx, while behind the receptaculum seminis and ovary lie in the concavity of a sort of recess between two very slight postero-lateral prolongations.

The walls of the intestine are deeply sacculated, a number of incomplete partitions running inwards from the body wall, as already described, and producing a series of circular constrictions, so that the internal cavity consists of a central space and a series of annular cæca lying between successive constrictions.

The intestinal wall (Plate XXI, fig. 7) is of considerable thickness. It is composed of greatly elongated epithelial cells (*e.*) with rounded inner ends which are devoid of cilia. In the granular substance of the cells themselves, as well as in little special reservoirs (*c.*), which appear to be intracellular, are very numerous large granules which show a distinct concentric structure ; these, which colour darkly with hæmatoxylin, but are little affected by carmine, are most numerous towards the bases of the cells. This epithelium is supported externally by a thin muscular coat (*m.*).

## EXCRETORY SYSTEM.

The excretory system of *Temnocephala* differs from that of most Trematodes<sup>1</sup> in opening on the exterior by two apertures. These are situated on the dorsal surface slightly behind the eyes, as already described. The surface in this position is usually found to be elevated on each side into a rounded eminence, and in the centre of this is easily to be distinguished the minute circular opening. This leads into the cavity of a non-ciliated sac (Plate XXI, figs. 9 and 10) with thick walls, of a pyriform shape, but slightly bent on itself. From the narrower posterior end proceed two large vessels which pass backwards along the lateral edge of the alimentary canal, and two (or a single one which speedily bifurcates) passing forwards towards the bases of the tentacles. As ordinarily seen these canals are twisted into spirals owing to the contraction of the whole body, but when the body is fully extended they are straightened out. The arrangement and final destination of these vessels and their branches I did not succeed in tracing. It would seem probable that the branches open directly into the spaces and channels in the parenchyma, and the "Schwingende Lappchen" found in other forms do not seem to be present.<sup>2</sup>

The above-described arrangement of the excretory system would seem to be very characteristic. Paired external openings, where they occur in other Trematodes, are to be found on the ventral and not on the dorsal surface, with the single doubtful exception of *Polystomum*.

The wall of the terminal sac (fig. 10) is composed of a thick layer of very finely fibrous substance (*e.*) without a trace of nuclei, but with occasional rounded vacuoles, and a thin layer of a similar substance lines the longitudinal vessels (fig. 11). External to this protoplasmic layer is a thin sheet of the parenchyma muscle (fig. 10, *m.*) which completely invests the

<sup>1</sup> Vide Fraipont's "Recherches sur l'appareil excréteur des Trematodes et des Cestodes," "Archives de Biologie," ii (1881).

<sup>2</sup> Taschenberg states that they are absent also in *Tristomum* (see 'Zoologischer Jahresbericht,' 1879, i, p. 319).



organ. The external aperture is capable of being dilated or contracted by specially arranged fibres of the muscular layers of the body wall. At the narrow end of the sac, where the branches are given off, are two large ganglion-cells (figs. 9 and 10, *g.*).

#### NERVOUS SYSTEM.

The cerebral ganglion (Pl. XXI, fig. 12, and Pl. XXII, fig. 1) is a six-sided body situated immediately beneath the longitudinal layer of muscle on the dorsal aspect, just in front of the pharynx. It consists of a clump of non-nucleated granular material, having ganglion-cells symmetrically arranged around it, with lateral, anterior, and posterior commissures of nerve-fibres. Laterally, it gives off in front a pair of nerve-trunks, each of which divides into three branches entering the tentacles—the middle tentacle being supplied by a branch from each side. Lateral branches pass outwards to supply the sides of the anterior region of the body. Posteriorly, the ganglion gives origin to three pairs of nerve-cords, which pass backwards towards the posterior end of the body. The ganglion bends downwards laterally towards the ventral aspect of the body, but the origin of the branches are still all distinctly dorsal in position. The first of these—the dorsal (Pl. XXI, fig. 12)—are the smallest, and are rather more superficial in position than the others. They leave the cerebral ganglion at its posterior and lateral angles, and run along on the dorsal aspect of the body immediately beneath the longitudinal layer of muscle in the pigmented “nervous” layer, the distance between the two cords being less than their distance from the lateral border. Branches are given off from these cords as they pass backwards, both internally and externally at frequent and fairly regular intervals. The internal branches of each cord pass inwards at right angles to the long axis of the body, and unite with the corresponding branch of the opposite side, sometimes after dividing into two. The external branches bifurcate again and again, the system of fine twigs thus produced anastomosing freely, and giving rise to a fine meshwork

of fibres. Finally, the longitudinal cords, much diminished in size, unite together near the posterior border.

The whole course of these dorsal cords and their branches can be made out much more readily than in the case of the others. If an alcoholic specimen of *T. fasciata* be macerated for a day or two in weak bichromate of potash and weak alcohol, and the cuticle, epidermis, and muscular layers, with the outer layer of pigment carefully stripped off, the nerves are readily traced by the light lines which they form among the pigment of the nervous layer. In young specimens of the same species in which the outer layer of pigment is imperfectly developed, more or less of the course of this series of nerves can usually be seen, and in the New Zealand *T. novæ-zelandiæ* in which the outer layer of pigment is little developed or absent, the nerves are readily traceable even in the adult. In the case of the other sets of nerves resort must be had in tracing them to the study of series of sections, and I am not able to give more than a general account of their distribution.

The second pair or dorso-lateral cords (Pl. XXI, fig. 4, and Pl. XXI, fig. 12, *d. l. n.*) run backwards on the dorsal aspect of the body immediately outside the testes, not far from the lateral border. It is of larger size than the dorsal, and sends off branches between the organs. The ventral cords (*v. n.*) are the largest. From the ganglion they curve round the pharynx and run along the ventral aspect in the angle between the testes externally, and rather farther from the median line than from the lateral border. The ventral and lateral longitudinal cords are connected by transverse branches, and the ventral cords of opposite sides are united similarly by numerous transverse commissures.

The nerve-fibres (Pl. XXII, figs. 2 and 3) of which these longitudinal cords and their branches consist, are large fibres averaging .01 mm. in diameter, of very delicate material, which is not readily acted on by staining agents, enclosed in a more resistant sheath. The central material shrinks greatly in preserved specimens, and this with its being little affected by dyes

very often gives the fibres the appearance of hollow tubes; when perfectly preserved it presents a reticulate appearance such as is represented in fig. 3; but this is very rarely to be observed. Within the sheath, besides the delicate substance constituting the nerve-fibre, there are also in the commissural nerves that form an important part of the cerebral ganglion, though not, so far as I have observed, in the course of the peripheral nerves, numbers of bipolar ganglion-cells.

This arrangement of the nervous system is, as regards the posterior part of it—the six longitudinal cords—very similar to that described by Lang as observed by him in the *Tristomidæ*.<sup>1</sup> The development of the tentacles in *Temnocephala*, and the consequent greater relative importance of the anterior region of the animal, are accompanied by a greater development of the nerves running forwards from the cerebral ganglion.

The single pair of eyes (Pl. XXI, fig. 13) are of extremely simple structure. They lie almost over the brain, so that the nerves which pass up to them are very short. The eye consists of a cup-shaped mass of dense pigment (*p.*), at the mouth of which are one or two nerve-cells (*g.*) not differing from those of the cerebral ganglion. Enclosed in the cup, the mouth of which is directed upwards and outwards, is a highly refracting body (*r.*) of a spherical form. This stains with difficulty and not very darkly, and is obscurely fibrillar in minute structure; it contains a nucleus near the mouth of the cup, and towards the base shows a trace of division into separate segments. Completely enclosed in the substance of the pigment of the cup on its inner side is a spherical cell (*t.*), of nearly the same dimensions as the body contained in the cavity of the cup; this exhibits a fine protoplasmic network and contains a solid-looking nucleus.

<sup>1</sup> "Untersuchungen zur vergleichenden Anatomie u. Histologie des Nervensystems der Platyelminthen," 'Mittheilungen aus der Zool. Station zu Neapel,' ii Band. A very similar arrangement is described in *Distomum isostomum* by E. Gaffron ("Zum Nervensystem der Trematoden," 'Zool. Beiträge,' herausg. v. A. Schneider, 1884, known to me through an abstract in the *Biologisches Centralblatt*, iv).

The tentacles are also to be regarded as sense organs as well as aiding in locomotion and prehension. There is nothing, however, in the structure of these organs, except the presence of large nerves, specially connected with their sensory functions; the epidermis and the muscular layers resemble those of other parts of the body.

#### REPRODUCTIVE ORGANS.

The common genital aperture (Pl. XX, fig. 5, *g.*) is a tolerably large slit-like opening situated a little distance in front of the sucker. It is surrounded by a special set of muscular fibres which serve the purpose of a sort of sphincter. It leads into a common genital cloaca, into which on one side projects the penis, while on the other is situated the female opening. This cavity is lined by a continuation of the cuticle and epidermis of the outer surface, the cells of the latter being, however, considerably elongated, forming an almost columnar epithelium, external to which is a thick layer of muscle.

The testes (*te.* in Pl. XX, fig. 6; Pl. XXI, fig. 4; and Pl. XXII, fig. 17) are two pairs of large glands of cylindrical form, with the long axis longitudinal, lying at the sides of the alimentary canal, and extending throughout the length of the body from the pharyngeal region to some distance behind the sexual aperture. The two testes of the same side are connected by a slender duct. They are invested with an extremely delicate layer of muscle, which is continued into the wall of the duct and of the vas deferens. Though there are only two pairs of testes, these partake to some extent of the segmented character of the animal—being partially subdivided at the sides by a deep transverse incision opposite each of the muscular partitions through which, however, the main substance of the gland is continued uninterrupted. The spermatozoa have pear-shaped heads, about  $\cdot 0046$  mm. in diameter, and slender flagella,  $\cdot 083$  mm. in length.

The two vasa deferentia are slender tubes, which, passing inwards from the posterior testes towards the middle line of the body, meet to form a large seminal vesicle or spermatoc



reservoir (Pl. XXII, fig. 17, *e. j.*), which is always found to be distended with spermatozoa. This is an elongated sac, much dilated proximally, which runs almost transversely from near the middle line of the body where the vasa deferentia open into it towards the right, and opening into the base of the canal of the penis. The latter organ (Pl. XX, fig. 6, *p.*) is contained, when retracted, in an elongated muscular sac lying transversely with the mouth directed towards the left and towards the dorsal side. It is a cylindrical, slightly curved, chitinous body, having a wider proximal and narrower distal end. In *T. fasciata* (Pl. XX, figs. 5—7) and *T. quadricornis* (Pl. XX, fig. 8) the distal end is provided with a knob or glans (*gl.*); in *T. minor* and *T. novæ-zelandiæ*, this is merely represented by a slight rim (Pl. XXII, figs. 9 and 10). The whole is enclosed in a sheath composed of circular and longitudinal muscular fibres—the latter the stronger, and enclosed by the former. At the opening of the penis the sheath is continuous with the proper chitinous wall of the organ, it is continuous also proximally with the sheath of the spermatheca and distally with the muscular investment of the genital cloaca. In *T. fasciata*, where it turns back to become continuous with the proper wall of the penial cylinder, it is provided with a number of chitinous spines, which, when the penis is retracted, lie in the interior of the terminal knob or glans in a radiating manner, their outer ends, which are the broader, embedded in the sheath and the acute inner ends pointing into the narrow lumen. When the penis is protracted this inverted part of the sheath will become everted, and the spine project on the exterior of the end of the penis, thus enabling the organ to retain a firm hold during the act of copulation. In *T. minor* and *T. novæ-zelandiæ* there is only a slight rim to effect this purpose; but in the latter species (Pl. XXII, fig. 19) the female opening is provided with inwardly directed spines, which doubtless effect the same object. The interior of the penis and spermatheca is lined with a protoplasmic layer containing nuclei, but without cell boundaries. Into the lumen of the ejaculatory duct there

is discharged the secretion of the unicellular glands already mentioned as apparently forming a part of the system of subcutaneous glands. The secretion consists of or contains little spherical, highly refracting bodies, which stain darkly with hæmatoxylin; probably the foreign particles found in the receptaculum seminis with the spermatozoa are the products of this secretion.

The female organs consist of receptaculum seminis, or single ovary, oviduct, uterus, vitelline, and uterine glands, together with certain of the subcutaneous glands opening around the sexual orifice, which probably secrete the viscid matter by means of which the eggs adhere together.

The receptaculum seminis (Pl. XX, fig. 6, *re.*, and Pl. XXI, fig. 8, *rec. sem.*) is a large rounded sac which lies in the middle line in a deep bay of the posterior wall of the intestine. Its walls are formed of a granular protoplasmic matter, without differentiation, into cells, but with large nuclei here and there. External to this is a thin layer of muscular fibres. In all the specimens examined the cavity of the sac was found to be full of spermatozoa, with frequently small particles of amorphous matter, probably derived from the accessory glands of the male organs.

Opening out of the left-hand corner of the receptaculum seminis is the oviduct (*o. d.* in Pl. XX, fig. 6; Pl. XXI, fig. 8; and Pl. XXII, fig. 12), a rather narrow, curved tube which opens below into the uterus. The wall of the oviduct (Pl. XXII, fig. 12) consists of an external circular and an internal longitudinal layer of muscular fibres, and is devoid of epithelium, but is lined internally with a homogeneous layer of some delicate non-nucleated material, which is not readily acted on by staining agents. Into its lumen open the ducts of a few of the shell-glands.

The wall of the uterus (Pl. XXI, fig. 8) resembles that of the oviduct in structure; but the muscular layer is thicker, and the fibres cross one another in all directions. Most of the shell-glands open into the uterus. Each shell-gland (*s. gl.*) is a single, irregularly-shaped cell of very large size, with a large

nucleus; passing from it to the oviduct or uterus is the narrow duct (*d.*), which is essentially a process of the cell substance. As the duct passes through the wall of the uterus it acquires definite boundaries, and presents a little vesicular enlargement (*d.*) just before it opens into the uterus. Leading from the uterus to the genital cloaca is the vagina, a short, narrow passage, which in *T. novæ-zelandiæ* is provided at its mouth with a series of chitinous teeth.

The vitelline glands (Pl. XXII, figs. 15 and 16) consist of a number of rounded lobules arranged in narrow branching lobes, which, for the most part, take a transverse direction. These lobes are very closely applied to the wall of the intestine, which they almost entirely cover, both on the dorsal and on the ventral aspect. The muscular septa pass outwards from the wall of the alimentary canal, and through between the lobules of the vitelline gland in such a way as to bring about an imperfectly metameric arrangement in irregular transverse lobes, which, however, branch and anastomose with one another. The arrangement of the lobes and the degree to which the glands are developed vary somewhat in different individuals. The lobules are invested in a thin layer of the parenchyma muscle, which is continuous with that constituting the septa, and similar to the layer investing the intestine. The central substance of the lobules is composed of large irregular cells with ill-defined boundaries, whose protoplasm is clear and colourless in the fresh state, but with a number of large granules which become more evident in hardened specimens; the nuclei resemble those of the alimentary epithelium; throughout the protoplasm there are frequently large rounded vacuoles.

The ovary (Pl. XXII, fig. 11) is an oval solid body .16 mm. in length, attached to the right wall of the receptaculum seminis, close to the beginning of the oviduct. The ova are narrow pyramids about .083 mm. in length, each of which passes transversely through the entire thickness of the ovary. The impregnated ova are received singly into the uterus, where they become surrounded by a considerable quantity of vitelline

matter, and become enclosed in a chitinous shell secreted by the shell-glands. The egg is now compared with the animal, a very large structure (as much as a sixth of the length of the animal), and greatly distends the walls of the uterus. When extended (Pl. XXII, fig. 18) it has a short stalk, by means of which it becomes attached to the shell of the crayfish, and is enclosed in viscid matter, which when it hardens serves to cement the eggs together. The eggs are found in considerable numbers from October to February, attached chiefly to the under surface of the abdomen, some also at the sides of the mouth and the lower edges of the branchiostegites. The development of the embryo has not yet been studied; there is, as in other ectoparasitic Trematodes, no metamorphosis. *Temnocephalæ*, perfect in every respect, being found still enclosed in the egg.

#### AFFINITIES OF TEMNOCEPHALA.

Though most nearly related to the *Tristomidæ*, *Temnocephala* presents so many special peculiarities that it becomes necessary to regard it as the type of a distinct family. The principal characteristic features in its structure may be summarised as follows :

The cephalic end of the body is produced into four, five, or six slender, filiform tentacles, which are capable of being used for prehension and touch, and in locomotion take the place of anterior suckers, their adhesive powers being increased by the secretion of certain special unicellular glands. There is a single, large, radiated posterior sucker without hooks. The body presents traces of a rudimentary form of segmentation in the shape of incomplete transverse dissepiments formed by specialised portions of the parenchyma muscle. The intestine is constricted at regular intervals by these septa; its epithelium is not ciliated. There are three pairs of longitudinal nerve-trunks, a dorsal, a dorso-lateral, and a ventral, connected by numerous commissures. The excretory system opens by two apertures, placed far forwards on the dorsal surface. There is a single genital aperture leading into a genital cloaca, into



which the ejaculatory duct and the vagina open ; there are two pairs of lobed testes, vitelline glands, which partake of the imperfect segmentation of the body, a single ovary, receptaculum seminis, oviduct and uterus.

The broader questions suggested by the imperfect segmentation of *Temnocephala*, and by other features in its organization which seem to point to a possible genetic relationship with the segmented worms, cannot well be dealt with until the development has been investigated.

## EXPLANATION OF PLATES XX, XXI, & XXII,

Illustrating Mr. William A. Haswell's paper "On *Temnocephala*, an Aberrant Monogenetic Trematode."

### PLATE XX.

FIG. 1.—*Temnocephala fasciata* in various positions. Natural size.

FIG. 2.—*Temnocephala fasciata*, from living specimens. Magnified.

FIG. 3.—*Temnocephala quadricornis*. Magnified.

FIG. 4.—*Temnocephala minor*, dorsal view, from preserved specimen. Magnified.

FIG. 5.—*Temnocephala minor*, ventral view. *g*. Genital aperture. *m*. Mouth. *s*. Sucker. *te*. Tentacles.

FIG. 6.—Diagram of the general organization of *Temnocephala*. *ph*. Pharynx. *i*. Intestine. *ex*. Excretory sac. *ex'*. Anterior canal of excretory system. *ex''*. Posterior canal of excretory system. *br*. Brain. *cl*. Genital cloaca. *te*. Testes. *v. d.* Vas deferens. *p*. Penis. *re*. Receptaculum seminis. *ov*. Ovary. *od*. Oviduct and uterus. *vit*. Vitelline glands. *s*. Sucker.

### PLATE XXI.

FIG. 1.—Transverse section through the body wall of *Temnocephala fasciata*. *c*. Cuticle. *e*. Epidermis. *b*. Basement membrane. *c. m.* Circularly arranged layer of muscular fibres. *p*. Pigment layer. *l. m.* Longitudinal layer of fibres. *par*. Parenchyma.

FIG. 2.—Longitudinal section of the ventral body wall, in the neighbourhood of the genital opening, to show the ducts of the subcutaneous glands, *d*. Other letters as above.

FIG. 3. Cells of subcutaneous glands.

FIG. 4.—Transverse section of a young specimen of *Temnocephala fasciata*, in the region of the genital cloaca and penis. *c*. Cuticle. *e*. Epidermis. *b*. Basement membrane. *p*. Pigment layer. *l. m*. Longitudinal layer of muscle. *par*. Parenchyma, with subcutaneous gland-cells and dorso-ventral muscular fibres. *d. l. n*. Dorso-lateral nerve. *v. n*. Ventral nerve. *cl*. Genital cloaca. *pe*. Penis. *vit*. Lobule of vitelline gland. *te*. Extremity of testis (here imperfectly developed).

FIG. 5.—Outline of the alimentary canal of a young specimen of *Temnocephala fasciata*. *ph*. Pharynx. *i*. Intestine.

FIG. 6.—Vertical section of the wall of the pharynx, from a longitudinal section of the body. *ep*. Internal layer of granular matter. *i. c. l*. Internal circular longitudinal layer of muscle. *i. c. t*. Internal circular transverse layer. *e. c. t*. External transverse. *e. c. l*. External longitudinal. *rad*. Radiating fibres. *g*. Ganglion-cells.

FIG. 7. Section of the wall of the intestine. *m*. Layer of muscle. *e*. Epithelium. *c*. Reservoirs of granules.

FIG. 8.—Longitudinal and vertical section of *Temnocephala minor*. *s*. Sucker. *v*. Ventral body wall. *d*. Dorsal body wall. *int*. Cavity of the intestine. *sept*. Septa. *vit*. Lobules of vitelline gland. *gl*. Subcutaneous gland-cells. *od*. Oviduct. *ut*. Uterus. *rec*. Receptaculum seminis.

FIG. 9.—Excretory sac of *Temnocephala fasciata* in the fresh condition, viewed from the dorsal aspect. *o*. External opening. *l. c*. Longitudinal canals. *g*. Nuclei of ganglion-cells.

FIG. 10.—Section of excretory sac, on a level with the external opening. *e*. Proper wall of sac, with vacuoles. *m*. Investing layer of muscle. *g*. Ganglion-cell.

FIG. 11.—Longitudinal section of posterior excretory canal.

FIG. 12.—Diagram of dorsal portion of nervous system, showing the arrangement of the tentacular nerves, and the dorsal longitudinal trunks with their branches and commissures.

FIG. 13.—Transverse section through the eyes of *Temnocephala fasciata*. *p*. Pigment cup. *r*. Contained substance. *g*. Ganglion-cells opposite the mouth of the cup. *t*. Peculiar cell enclosed in the pigment of the optic cup. *u*. Large cells lying between the eyes.

## PLATE XXII.

FIG. 1.—Transverse section through the brain ganglion of *Temnocephala fasciata*.

FIG. 2.—Transverse section of a portion of the ventral nerve.

FIG. 3.—Longitudinal section of nerve-fibre from dorsal nerve-plexus.

FIG. 4.—Elements of testis.

FIG. 5.—Penis and penis-sheath of *Temnocephala fasciata*. *cl.* Genital cloaca. *sh.* Penis-sheath. *gl.* Terminal enlargement of "glans."

FIG. 6.—Transverse section of the distal end of the penis of *Temnocephala fasciata*, through the "glans." *sh.* Sheath. *sp.* Inverted chitinous spines.

FIG. 7.—Oblique section through spermatic reservoir, penis, and penis-sheath of *Temnocephala fasciata*, from a horizontal section of the body. *cl.* Genital cloaca. *sh.* Sheath. *ej.* Spermatic reservoir (ejaculatory duct).

FIG. 8.—End of penis of *Temnocephala quadricornis*.

FIG. 9.—End of penis of *Temnocephala minor*.

FIG. 10.—End of penis of *Temnocephala novæ-zelandiæ*.

FIG. 11.—Ovary of *Temnocephala fasciata*.

FIG. 12.—Transverse section of the oviduct of *Temnocephala fasciata*. *c. m.* Circular layer of muscle. *l. m.* Longitudinal layer of muscle. *p.* Internal homogeneous substance. *f.* Investing reticulum of fibrous tissue.

FIG. 13.—Vertical section of the wall of the uterus in the same species, with the shell-glands and their ducts. *s. gl.* Shell-glands. *d.* Ducts. *d'.* Terminal enlargements of the ducts. *m.* Muscle. *p.* Thin internal homogeneous layer.

FIG. 14.—Oblique section of uterine wall nearly parallel with the surface, showing the terminal dilatations of the ducts of the shell-glands with the investing plexus of muscular fibres.

FIG. 15.—Outline of the ventral part of the vitelline glands of *Temnocephala fasciata*. *i.* Outline of the wall of the intestine.

FIG. 16.—Section through a lobule of the vitelline glands. *m.* Investing layer of muscular fibres. *v.* Vacuoles in the protoplasm of the gland-cells.

FIG. 17.—Portion of a transverse section of a young specimen of *Temnocephala fasciata*, just behind the pharynx. *c.* Cuticle. *e.* Epidermis. *b.* Basement membrane. *l. m.* Longitudinal layer of muscle. *v. l. m.* Ventral longitudinal layer of muscle. *par* Parenchyma, with subcutaneous glands. *d. v. m.* Dorso-ventral bundles of muscular fibres. *d. l. n.* Dorso-lateral nerve. *v. n.* Ventral nerve. *int.* Intestine. *te.* Anterior end of testis.

FIG. 18.—Eggs of *Temnocephala fasciata*. Magnified.

FIG. 19.—Opening of the vagina of *Temnocephala novæ-zelandiæ*.

**Notes on Echinoderm Morphology, No. XI. On the Development of the Apical Plates in *Amphiura squamata*.**

By

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SOME very important observations "On the Development of the Calcareous Plates of *Amphiura*" have been recently published by Dr. J. W. Fewkes,<sup>1</sup> who has also entered into a discussion respecting the morphological relations of these plates. *Amphiura squamata* is viviparous, and the young undergo a direct or abbreviated development without passing through a definite Pluteus form, so that it is easy to follow the various larval stages and to study the mode of appearance of the skeletal plates.

Ludwig took up the subject in 1881,<sup>2</sup> and made the very striking discovery that two rings of radially situated plates are developed around the dorsocentral. Those of the distal ring are carried outwards from the disc at the ends of the growing arms, and are known as the terminals (fig. 1, r); while the five plates of the proximal ring (4) remain on the disc close to the dorsocentral (1), and with it develop into the rosette of six primary plates which is a prominent feature on the abactina. surface of many adult Ophiurids. In *Amphiura squamata* two more rings of plates, the intermediate plates of Ludwig, eventually appear between these radials and the dorsocentral;

<sup>1</sup> 'Bull. Mus. Comp. Zoöl.,' 1887, vol. xiii, No. 4, pp. 107—150, pl. i—iii.

<sup>2</sup> "Zur Entwicklungsgeschichte des Ophiurenskelettes," 'Zeitschr. f. wiss. Zool.,' 1881, Bd. xxxvi, pp. 181—200, Taf. x, xi.



and I expressed my belief in 1882<sup>1</sup> that they respectively represent the under-basals and basals of the dicyclic Crinoids (fig. 11, 2, 3). Two years later I pointed out the presence of this dicyclic base in various adult Ophiurids<sup>2</sup>; while the important discovery was announced by Sladen that it likewise occurs in many Asterids, both larval and adult, and also that in this group, just as in the Ophiurids, there are primary radial plates which remain on the disc while the terminals are carried outwards on the growing arms.<sup>3</sup>

These primary radial plates of Asterids and Ophiurids, including *Amphiura*, were homologised by both Sladen and myself with the first radials of the Crinoidea, the correspondence of which with the ocular plates of the Urchins had been long ago pointed out by Agassiz, Lovén, and others. No one had questioned this latter comparison, and it appeared equally indisputable that the primary radials of *Amphiura* were also homologous with the ocular plates of an Urchin, despite the relation of the latter to the eye-spot, a relation which is not characteristic of the primary radials in either of the three groups of brachiote Echinoderms.

The subject has been lately reopened by Fewkes,<sup>4</sup> who says:—

“The question which plates in the young *Amphiura* correspond to the oculars of sea-urchins, assumes a new phase in the light of what we know of the permanent retention of the radials in the abactinal hemisome of the body of *Amphiura*, and the relation of the terminals to the primitive tentacle. Now that we know that the primary radials of *Amphiura* are

<sup>1</sup> “Notes on Echinoderm Morphology,” No. V: “On the Homologies of the Apical System, with some Remarks upon the Blood-vessels,” ‘Quart. Journ. Micr. Sci.,’ 1882, vol. xxii, New Ser., p. 380.

<sup>2</sup> “Notes on Echinoderm Morphology,” No. VII: “On the Apical System of the Ophiurids,” ‘Quart. Journ. Micr. Sci.,’ 1884, vol. xxiv, New Ser., pp. 4, 11.

<sup>3</sup> “On the Homologies of the Primary Larval Plates in the Test of Brachiote Echinoderms,” ‘Quart. Journ. Micr. Sci.,’ 1884, vol. xxiv, New Ser., pp. 29, 34.

<sup>4</sup> Loc. cit., p. 124.

not pushed out to the extremity of the rays, but always remain in the disk, and that another set of plates (terminals) do suffer this change, we have this difficulty in a comparison of the young Echinoid with the young *Amphiura*. The terminals of *Amphiura* are independent centres of calcification from the radials. If terminals and radials in *Amphiura* lie in the same radius, how can the one or the other, especially the former, be the same as the oculars of the sea-urchin?"

I must confess that I do not quite understand what "new" phase this question has assumed since I wrote on the subject in 1882. All the facts to which Fewkes refers in the above passage were then known, having been discovered by Ludwig in the previous year; and it was these very facts which led me to homologise the primary radials of *Amphiura* and of the Ophiurids generally with the oculars of an Urchin. Sladen has accepted this view, and I am not aware of its ever having been disputed.<sup>1</sup> I fail to see therefore what the new phase of the question may be to which Fewkes refers; for the fact which he mentions, that the radials of Ophiurids are not perforated for the eye-spots, like the oculars of an Urchin, is familiar to all Echinoderm students.

The radials of a Crinoid are equally devoid of any relation to the ambulacral structures, and yet they have been always regarded as homologous with the oculars of an Urchin by every writer who has dealt with the subject; and Fewkes<sup>2</sup> arrives at the same conclusion as Sladen and myself had previously done, that "it seems more natural to compare radials in *Amphiura* with oculars in sea-urchins, notwithstanding the

<sup>1</sup> Fewkes refers, somewhat unnecessarily, "to those who compare the terminals of starfishes and brittle stars without pluteus with the ocular plates of the sea-urchin." I know of no writer who has done so since the publication of Ludwig's and Sladen's discoveries respecting the development of both radials and terminals in Ophiurids and Asterids. Neither has anyone, that I am aware of, suggested that either terminals or radials of *Amphiura* are comparable to the genitals of the Urchins, though Fewkes takes some trouble to point out the very obvious impossibility of such an homology (p. 125).

<sup>2</sup> Loc. cit., p. 126.

position of the eye-spot." One or two further arguments may be adduced in favour of this view.

1. The embryonic radials of Ophiurids always remain upon the abactinal surface of the adult in the neighbourhood of the dorsocentral, and in many species develop into large plates, the primaries, which form a closed ring around the dorsocentral, just as in the early stages of the young *Amphiura* (fig. 1, 4), though they are sometimes separated from it by intermediate

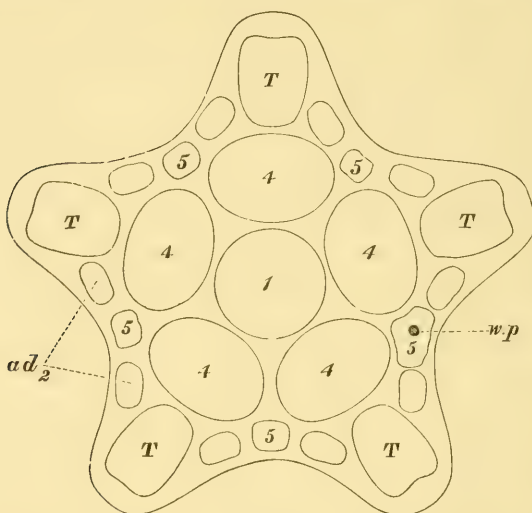


FIG. 1.—('Quart. Journ. Micr. Sci.,' 1882, vol. xxii, p. 379.) Apical system of the young *Amphiura squamata*; Stage I, after Ludwig. 1. Dorso-central. 4. Radials. 5. Orals. T. Terminals. *ad*<sub>2</sub>. Second adambulacral plates. *w. p.* Water-pore.

plates (fig. 11, 2, 3). The oculars of an Urchin are also confined to the abactinal surface, and are separated from the dorsocentral by one ring of plates; while in most Crinoids the radials form a closed ring as in the earliest *Amphiura*, sometimes with one and sometimes with two rings of plates within them, just as in the two subsequent stages of the development of *Amphiura*.

On the other hand, the terminals of Ophiurids never form a closed ring of plates, but are well separated laterally from their very first appearance, and become more and more separated as the growth of the arms carries them away from the disc.

2. Sladen has shown that there are both terminal and radial plates in the young Asterid, just as in the young Ophiurid, and, like all his predecessors, he regards the terminals of Asterids as homologous with those of Ophiurids, although the latter have no eye-spot. If this homology be admitted—and I do not know of its ever having been disputed—we have an exactly similar case to that of the Ophiurid radials and the oculars of an Urchin, the one set of plates being associated with an eye-spot and the other not, although they are mutually homologous.

We may then, I think, assert, without fear of contradiction, that the radial plates are mutually homologous in Ophiurids and Urchins, Asterids and Crinoids, and also that the relative time of their appearance is of no general morphological importance. They appear before the basals in the Ophiurids, but after them in the other three groups, being also anticipated in Asterids<sup>1</sup> and Crinoids,<sup>2</sup> and probably in the Urchins as well, by the dorsocentral.

Thus then, so far as concerns the primary radial plates of

<sup>1</sup> On pp. 124, 127 Fewkes refers to the works of Agassiz and Balfour as apparently proving that the radials of Starfishes appear before the dorsocentral. He forgets, however, that the plates which were formerly described as the radials of Starfishes are now known to be the terminals, and that the true radials do not appear till after the basals and the dorsocentral, as shown by Sladen.

<sup>2</sup> Fewkes remarks that "it is difficult to compare the centrodorsal of Crinoids with the dorsocentral of the Ophiuran" (p. 127). But why make the attempt? There is a dorsocentral in Crinoids perfectly homologous with that of the Ophiuran, as pointed out by Sladen and myself. But it is at the bottom of the larval stem, and altogether different from the cirrus-bearing top stem-joint or centro-dorsal. The distinction between the two was explained in this Journal as long ago as 1878; and the homology of the terminal plate at the base of the Crinoid stem with the dorsocentral of the Echinozoa has been frequently noticed since then by Lütken, Duncan and Sladen, Wachsmuth and Springer, Etheridge and myself. I am at a loss to understand therefore why Fewkes refers to the Crinoid centro-dorsal, but omits all notice of the dorsocentral.



the apical system, Fewkes's views are those of his predecessors, as indeed he himself admits. But he adds a suggestion which he considers as a direct sequence of the homology of the primary radials in Ophiurids and Crinoids, respectively.<sup>1</sup> It is this: "The homology of the radial shields of the *Amphiura* with the first brachials of the Crinoid would seem not unreasonable. The only paired plates of the arms with which they could be compared are the adambulacral. With these, however, they have little resemblance save in their double origin." If, as I suppose, Fewkes uses the term "first brachials" to denote the lowest joints of the two arms which are borne upon the radial axillaries of *Pentacrinus*, *Antedon*, and most recent Crinoids, there are at least three objections to an homology between them and the radial shields of the Ophiurids.

1. Many Crinoids, e.g. *Hyocrinus*, *Rhizocrinus*, *Eudiocrinus*, *Cupressocrinus*, &c., have no paired first brachials at all, for there are only five arms, one on each primary radial.

2. In those Crinoids which have ten or more arms there may be from one to seven radial plates between the primary or calyx-radials and the paired first brachials. The only genera in which the latter plates ever rest directly on the primary radials are the aberrant *Allagecrinus* and *Tribrachioocrinus*. But this is not the case all round the cup, so that there are never ten first brachials to correspond to the ten radial shields which are so constant in Ophiurids. Then, again, each of the two larger radials in *Catilloocrinus* may support as many as thirty arms. Where are the homologues of the two radial shields among all these first brachials?

3. The radial shields of Ophiurids are invariably present, but they have no permanent relations to the primary radials. It is not unlikely that they are always developed immediately outside the primaries, where they remain in many species. But, on the other hand, they are often separated from the primaries by a series of intermediate plates which exhibit no general constancy of arrangement, and cannot therefore be directly

<sup>1</sup> Loc. cit., p. 130.

compared to the single row of outer radials which presents itself so frequently in the Crinoids.<sup>1</sup>

These three considerations seem to me to indicate pretty clearly that it is useless to seek for the homologues of the radial shields in Ophiurids among the post-radial plates of Crinoids, more especially as we have not yet been able to identify them in any Asterid; and I prefer to regard them, like the terminals of both Ophiurids and Asterids, as plates which have no representatives in the Crinoidea.

Fewkes also discusses the homology of those intraradial or adaxial plates in the young *Amphiura* which I have regarded as homologous with the basals of Crinoids (figs. I—III, 3); and he suggests some doubts as to whether these plates "are basals in preference to other interrarial plates."<sup>2</sup>

The plates in question have an interrarial position within the ring of radials, i. e. between them and the dorsocentral; and at one stage of development they are the only adaxial interrarial plates (fig. III, 3). They thus correspond exactly to the basals of monocyclic Crinoids, and to the so-called genitals of Urchins and Asterids. In a large number of Ophiurids they develop into large plates which form a closed ring round the dorsocentral, with the radials immediately outside them, precisely as in the apex of an Urchin, or the calyx of a stemless Crinoid like *Uintacrinus*. Fewkes must surely be aware of this fact, for there are numerous figures illustrating it in Lyman's report on the "Challenger" Ophiurids; and it has formed the subject of much discussion by Sladen and myself. He supports his doubts by no arguments whatever, and entirely overlooks the important fact that the interradians of a Crinoid never form a closed ring within the circle of radials; for the only inter-radially situated plates which occupy such a position are the basals. It was this fact

<sup>1</sup> I am quite ready to admit, however, that the outer radials and the brachials of a Crinoid are in a general way represented in the Ophiurid by the upper arm-plates, and the row of median plates beyond the radial primaries which occur in *Ophiomusium*, *Ophioglypha*, and other genera.

<sup>2</sup> Loc. cit., pp. 129, 146.

which led me to suggest that these first formed plates between the radials and the dorsocentral of the young *Amphiura* are the homologues of the Crinoidal basals and of the so-called genitals in Urchins and Asterids; and the six years' work by myself and others since this suggestion was made has only served to make me more confident of its truth.

Ludwig gave a very clear description<sup>1</sup> of the appearance of these inter-radially placed basals in the young *Amphiura*, and he pointed out how at a later stage a set of radially situated plates appears between them and the dorsocentral. He illustrated both conditions by figs. 24 and 25 of his series, the latter showing five and the former ten plates between the dorsocentral and the radial primaries. Fig. 24, which I here repeat (fig. 11), was copied by myself for the purpose of

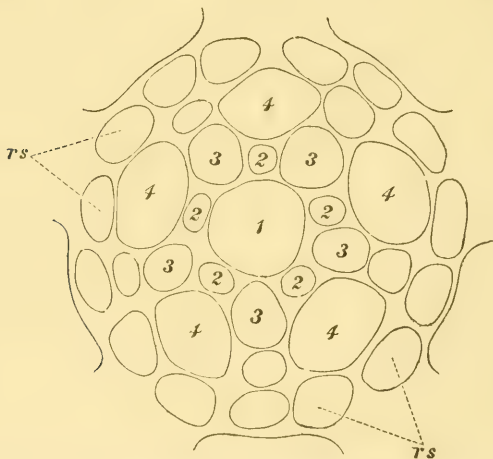


FIG. II.—('Quart. Journ. Micr. Sci.,' 1882, vol. xxii, p. 380.) Apical system of the young *Amphiura squamata*; Stage III, after Ludwig. 1. Dorsocentral. 2. Under-basals. 3. Basals. 4. Radials. *r. s.* Radial shields.

demonstrating that plates corresponding in position to the under-basals of a Crinoid (2) were developed in the young

<sup>1</sup> Loc. cit., p. 195.

Amphiura, as well as those corresponding to the basals (3). Fewkes<sup>1</sup> thinks, however, that it would have been better "in considering the relationship of the basals in the young Amphiura and their homologues in the projection of the calyx of an Antedon larva" if I had copied Ludwig's fig. 25 instead of his fig. 24, i. e. that showing the monocyclic and not the dicyclic stage of Amphiura. It is curious that he fails to see the reason why I copied the figure of the older, in preference to that of the younger stage. Homologues of the Crinoidal basals had long been recognised in the so-called genital plates of Urchins and Starfishes. But up to the time of the publication of Ludwig's memoir, representatives of the under-basals of a Crinoid<sup>2</sup> were not known to exist in any of the Echinozoa; and it was for the purpose of demonstrating their presence in Amphiura that I copied the figure of the older and dicyclic condition rather than that of the younger and monocyclic one, with the remark,<sup>3</sup> "The plates in the outer ring (fig. 11, 3) are inter-radial, while those of the inner ring next the dorso-central are radial in position (fig. 11, 2). In these plates we have, I believe, the representatives of the diacyclic base of Marsupites and other Crinoids, viz. a proximal ring of under-basals hitherto unknown in any of the Echinozoa, and a distal ring of interradial plates corresponding to the basals of the Crinoid and the genitals of the Asterid or Urchin, which have not been previously discovered in an Ophiurid."

The doubts which seem to have occurred to Fewkes respecting the homologies of the adaxial ring of interradial plates in

<sup>1</sup> Loc. cit., p. 129.

<sup>2</sup> While this paper was in the press an important discovery was announced by Mr. H. Bury at the Manchester meeting of the British Association. He has found under-basals in the ciliated larva of *Antedon rosacea*; but they soon fuse with the top stem-joint (centro-dorsal), and all trace of them is lost when the cirri appear. This is a very striking confirmation of the views of Messrs. Wachsmuth and Springer, whose palæontological studies had led them to express the belief that under-basals might be present in the early larva of *Comatulæ*.

<sup>3</sup> 'Quart. Journ. Micr. Sci.,' 1882, vol. xxii, New Ser., p. 380.



the young *Amphiura* which I have described as basals (figs. II, III, 3) appear to me to be due to the fact that the sequence of development of the apical plates is not the same in the American as in the European variety of *Amphiura squamata*. According to the description and figures of Ludwig the order in the latter form is as follows:—i. Radials (4); ii. Dorsocentral (1); iii. Basals (3); iv. Primary interradials (I.), and Under-basals (2); and v. Radial shields (*r. s.*). The under-basals and primary interradials seem to develop almost contemporaneously, fig. III showing two under-basals (2) in two rays between the dorsocentral (1) and the radials (4), and

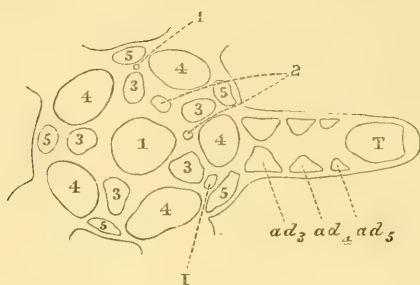


FIG. III.—Apical system and one arm of the young *Amphiura squamata*; Stage II, after Ludwig. 1. Dorsocentral. 2. Under-basals. 3. Basals. 4. Radials. 5. Orals. I. Primary interradials. T. Terminals.  $ad_3$ ,  $ad_4$ ,  $ad_5$ . Side arm-plates (adambulacra).

two very unequal abaxial or primary interradials (I.) each of them between a basal (3) and what I take to be an oral (5).<sup>1</sup>

This figure also shows that the fifth pair of side arm-plates

<sup>1</sup> It is just possible that this interpretation may be erroneous, and that the plates which are marked as orals (5) in the above diagram are really the primary interradials, and should be marked (I.). I do not think this probable, however, as this individual is so little older than that figured by Ludwig in his fig. 25, in which the orals are still quite distinct on the margin of the dorsal surface. But if the plates in question be interradials appearing thus early, the contrast between the times of development of the interradials and radial shields in the American and European forms respectively is even greater than I have described above. Fewkes agrees with me in thinking that they are probably orals.

(adambulacrals, *ad<sub>5</sub>*.) appear about the same time.<sup>1</sup> It is evident therefore from fig. III that the basals (3) reach a comparatively large size before the appearance of either inter-radials (I.), under-basals (2), or radial shields, and that the latter do not appear till after the formation of two at least of the under-basals and interradials.

From Fewkes's descriptions and figures, however, it would seem that the radial shields appear much earlier in the American variety, and that the developmental sequence is altogether different from that described by Ludwig for the European form. Fewkes's account is a little difficult to follow, owing to a want of precision in his terminology. Thus, for example, he three times uses the names "basals" and "inter-radials" as if they were synonymous; though every previous writer upon the calyx of the Crinoids and its relation to that of other Echinoderms has regarded the interradials and basals as fundamentally distinct in their morphological relations.

The earliest plates to appear in the inter-radial areas are the orals (figs. I, III, 5) which, as Fewkes himself describes on p. 128, are "forced to the actinal surface of the disc before the interradials arise." He speaks of the latter, the first inter-radials, as forming "on the periphery of the abactinal hemisome on interradial between contiguous radialia. They are triangular in shape, and occupy a triangular interspace between adjoining primary radialia." He calls them, however, abaxial basals or abaxial interradials, and they are designated in his figure by the letters *r p*<sup>2</sup>. (fig. IV, I). But as they are situated on the periphery of the abactinal hemisome outside the closed ring of radial primaries, it is altogether incorrect to speak of them as "basals." This term is only applicable to the ring of interradial plates which are situated adaxially to the primary radialia, i. e. between them and the dorsocentral (figs. II, III, 3). The basals of a monocyclic Crinoid, as implied in their name, which was given to them by Johannes

<sup>1</sup> The reader will do well to remember that the first two pairs of adambulacrals are on the ventral surface of the disc at this stage, and are therefore not visible in its dorsal aspect.

Müller, are the nearest to the vertical axis of the calyx of all the plates in the interradial areas ; and the term abaxial basals

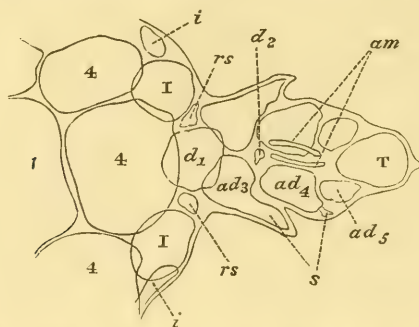


FIG. IV.—Dorsal view of one ray of the young *Amphiura squamata*; Stage II, after Fewkes. 1. Dorsocentral. 4. Radials. I. Primary inter-radials. *i*. Other interradials. *r. s.* Radial shields. *am*. Ambulacral plates. *d*<sub>1</sub>, *d*<sub>2</sub>. Upper arm-plates (dorsals). *ad*<sub>3</sub>, *ad*<sub>4</sub>, *ad*<sub>5</sub>. Side arm-plates (adambulacrals). *s*. Their spines.

is thus self-contradictory. The proximal ring of interradially situated plates or basals (figs. II, III, 3) cannot be called abaxial; and the interradial plates belonging to a distal or abaxial ring (fig. IV, I) are most certainly not basals. The term adaxial interradials is an expressive (but lengthy) name for the basals (3), as it implies that they lie within the ring of radials (4). But “abaxial basals” as a synonym for the interradial plates (I) beyond this ring is an impossibility; and the use of the term by a trained morphologist like Fewkes has surprised me considerably.

According to his description<sup>1</sup> the true basals or adaxial inter-radials seem to be the second set of plates to be developed inter-radially in the apical system of the American *Amphiura*, arising “in the corners left between the dorsocentral and contiguous radialia.” But before this happens the radial shields and two upper arm-plates have made their appearance (fig. IV, *r. s.*; *d*<sup>1</sup>, *d*<sup>2</sup>). At any rate this is how I should interpret Fewkes’s fig. 19, which is copied in fig. IV. But it has puzzled

<sup>1</sup> Loc. cit., p. 128.

me considerably, as he has omitted to letter the two plates next to the radial primary of the ray which he figures. I have marked them (4), regarding them as the primaries of the adjoining rays. But from his remarks on p. 128, which I have just quoted, it seems possible that they may be his adaxial interradians, i.e. the true basals, which appear before the radial shields, and not after them, as I have—perhaps erroneously—supposed. On the other hand, he states on the same page that a third ring of interradians “arises between the last-formed interradians and the periphery of the dorso-central.” Which does he consider as representing the Crinoidal basals? The second, or the third ring which is the most adaxial? There is not a single reference to his figures in the whole course of his description on p. 128 of the development of the plates in the interradian areas, and I have therefore found much difficulty in understanding it. I say this because I wish to apologise in advance if I have misinterpreted his statements.

The under-basals, which are formed comparatively early in the European *Amphiura squamata*, do not seem to appear in the American variety till the radial shields have reached some size. If we take the number of adambulacral plates as a criterion, we find that the European form with three of these plates (fig. III), has five basals, two under-basals, and two interradians,<sup>1</sup> but no radial shields; while the American form at the same stage has small shields and large interradians, but neither basals (?) nor under-basals (fig. IV). The differences in the sequence of formation of the apical plates in the two types may be summarised as follows:

## EUROPEAN :

- Radials (4).
- Dorsocentral (1).
- Basals (adaxial interradians, 3).
- { Abaxial interradians (1).
- { Under-basals (2).
- Radial shields (*r. s.*).

## AMERICAN :

- Radials (4).
- Dorsocentral (1).
- Abaxial interradians (1).
- <sup>2</sup> Radial shields (*r. s.*).
- <sup>2</sup> Basals (adaxial interradians, 3).
- Under-basals (2).

<sup>1</sup> See note 1 on p. 312.

<sup>2</sup> It is possible that these two should be interchanged.



Curiously enough, this considerable difference in the order of formation of the principal apical plates in the American and European varieties of one and the same species does not seem to have attracted Fewkes's attention. Had it done so, I cannot but think that several passages in his memoir would have been differently expressed. Thus, for example, in discussing the nature of the dorsocentral on p. 123, he says: "If, however, in Echinoids this plate forms before the ocular and genitals, and in *Amphiura* after the same, one is tempted to ask whether they are homologous. One might, of course, avoid the difficulty by the truism that the relative time of development is of little consequence, and that the appearance of the plate in *Amphiura* is simply retarded. Such an escape from the difficulty does not give much satisfaction, even if we remember the abbreviated development of *Amphiura*." But since the under-basals (and basals?) appear after the radial shields in the West Atlantic, and before them in the Mediterranean, the late appearance of the dorsocentral in *Amphiura* as compared with the Urchins, is no argument whatever against the view that this plate is homologous in the two groups; and in fact if the relative time of appearance of the Apical Plates is to be taken as a criterion of homologies, it is scarcely worth while for us to attempt to arrive at a general understanding of the Apical System of Echinoderms.

Another point of the same nature is the discrepancy between the descriptions given by Fewkes and Ludwig respectively of the relative times of formation of the radials and terminals. Ludwig<sup>1</sup> thinks it probable that the terminals appear before the radials; while Fewkes<sup>2</sup> believes the reverse to be the case, from the comparative sizes of the plates, though he admits that he has never seen a young *Amphiura* "with radials and without terminals." But if we may judge from the analogy of the under-basals and radial shields it would appear that both observers may be in the right.

This is still more probable with regard to the development

<sup>1</sup> Loc. cit., p. 187.

<sup>2</sup> Loc. cit., p. 139.

of the upper arm-plates. Fewkes says on p. 145: "I am led to suppose that the dorsals have been inadvertently omitted in certain of the figures of a young *Amphiura* by Ludwig (pl. xi, figs. 21, 25), for he has not represented these plates in a young specimen in which three pairs of side arm-plates are represented (pl. xi, fig. 21, *ad*<sup>3</sup>, *ad*<sup>4</sup>, *ad*<sup>5</sup>).<sup>1</sup> In a young *Amphiura* of about the same age (pl. iii, fig. 19)<sup>2</sup> at least one dorsal plate is formed, and in another as old as that represented in his fig. 25 (same plate) the dorsals have increased in number.<sup>3</sup> In none of Ludwig's figures are dorsals represented, though in figs. 21, 25, they must have been already formed." Fewkes makes substantially the same statement in his concluding summary on p. 147, "Dorsals are omitted in all Ludwig's figures of the arm from the abactinal side. My figure is younger than his (pl. xi, fig. 21), in which a dorsal ought to be represented."

It was, however, expressly noted by Ludwig<sup>4</sup> that "In Stadien welche nicht älter sind als das in fig. 21 gezeichnete, sind noch gar keine Dorsalplatten vorhanden, obgleich schon drei freie Armglieder angelegt sind."

This passage must have altogether escaped Fewkes's notice, or he would otherwise have scarcely have hinted at an inadvertent omission on the part of Ludwig, or have written so positively as to what plates ought or ought not to be represented in a particular developmental stage; while he makes no reference on his own part to the differences in the time of appearance of the radial shields, which are revealed by a comparison of his own observations with those of Ludwig, a fact which may eventually turn out to be of very considerable interest.

<sup>1</sup> This is copied as fig. III of the present communication (p. 312).

<sup>2</sup> Fig. IV, on p. 314.

<sup>3</sup> There is something wrong about this comparison. For Ludwig's fig. 25 represents a younger and not (as Fewkes implies) a later stage than fig. 21. There are not likely to be more dorsal plates developed in a form with two adambulacra (fig. 25) than in one with three (fig. 21).

<sup>4</sup> Loc. cit., p. 190.



The Photospheria of *Nyctiphanes Norvegica*,  
G. O. Sars.

By

**Rupert Vallentin**

and

**J. T. Cunningham, B.A.,**  
Fellow of University College, Oxford.

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With Plate XXIII.

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IT has long been a familiar fact to zoologists that in nearly all the Schizopodous genera which form the family Euphausiidæ are present ten small globular, reddish organs, having a resemblance in many respects to such eyes as those of Vertebrata and some Mollusca and Chaetopoda. The organs in question have not the least resemblance to the typical compound eye which is so characteristic of Arthropoda, but because when one of them is examined in the fresh state, a doubly convex structureless lens, and a cell layer suggesting the idea of a retina, are easily seen, therefore the organs were, until a recent date, generally denominated accessory eyes, or in German "Nebenaugen."

One of the earlier descriptions of the organs is in a paper by Claus<sup>1</sup> published in 1863. He says there that one of the conspicuous characters of Euphausia is the presence of accessory eyes, some of which are median unpaired, some lateral and paired. In proceeding to give an account of the structure

<sup>1</sup> "Ueber einige Schizopoden und niedere Malacostraken Messina's," 'Zeit. f. wiss. Zool.,' Bd. xiii, 1863.



of these "eyes," Claus points out that they had previously been seen by Dana<sup>1</sup> and Semper,<sup>2</sup> the latter of whom judged them to be eyes, and by Kroyer,<sup>3</sup> who found them in a form which he named *Thysanopoda inermis*, and thought they were probably auditory organs. The species in which Claus examined the organs was one occurring abundantly at Messina; he named it *Euphausia Mülleri*. He states that the organs were present on the basal joint of the second and seventh pair of thoracic appendages, and between the two members of each of the four anterior pairs of abdominal swimming feet, so that they were eight in number, two pairs and four median. They were reddish, pigmented, cylindrical bodies, whose immediate relation to the ganglia of the nerve-cord testified to their importance as sense organs. Although Claus did not succeed, notwithstanding earnest and repeated endeavours, in tracing out the nerve-endings, he concluded from the whole structure, and from the presence of lenses and muscles which rolled the organs to and fro, that in all probability they were movable organs of vision. The structure of all the organs was similar. Each bulb lay in a hemispherical protuberance of the body covering, fastened by slender threads, and movable by several oblique muscle-strands. The external wall of the bulb was formed by a cuticular envelope to which the threads and muscles were fastened, while the internal parts were more complicated. The front part of the contents consisted of a transparent kind of vitreous body, bounded behind by a glistening ring containing a lens. Behind the lens, followed in the centre of the "eye," a likewise highly refractive striated body composed of a number of closely packed rods. This body was enveloped in a clear spherical layer, whose posterior half fitted into a coarse pigmented fibrous membrane. This latter was in immediate contact with the wall of the bulb, and had the form of a hemispherical pigmented cup, open in front;

<sup>1</sup> 'Expl. Exped. of the United States,' "Crust. I," p. 639.

<sup>2</sup> "Reisebericht," 'Zeit. f. wiss. Zool.,' Bd. xii, 1862.

<sup>3</sup> "Forsøg til en monog. Fremst. af slaegt. Sergestes," 'Kon. Dansk. Vid. Selsk. Skrifter,' p. 294, 1859.

it held the position of a choroidea with regard to the transparent nucleated sphere. Claus could say nothing as to the significance of the transparent layer with its bundle of rods, but believed it to be the percipient element, although he could not trace any relation between it and nerves.

The pair of similar organs which are present behind the facettèd cornea in the eye-stalks in the adult, escaped Claus's notice; but in the young larvæ he mentions a bundle of rods behind each eye, which were obviously the anterior pair at an early stage of development, though he did not recognise the identity. Indeed, he was not likely to do so, for he could not have expected to find an accessory eye in immediate contact with the principal eye.

His description is illustrated by small figures which are drawn from the appearance of the organ in the fresh state *in situ*, and accordingly do not adequately exhibit the minute structure.

The species *Nyctophanes norvegica*, on which our observations were exclusively made, was first defined by Michael Sars in 1863<sup>1</sup> as *Thysanopoda norvegica*, and his diagnosis of the red spherical organs agrees exactly with the account given of them by Claus in 'Euphausia Mülleri:' "Organa in ventre existunt octo sensitiva (haud dubie oculi simplices) sphaerica, cornea transparente semiglobosa, cæterum laete purpure pigmentata, intus lente discretæ crystallina lenticulari."

It is surprising that in the numerous works published between 1840 and 1880, in which species belonging to the Euphausiidae are described and their accessory eyes mentioned, no allusion is made to any emanation of light from the animals, or to the possibility that the supposed additional eyes are really phosphorescent organs, notwithstanding the fact that J. Vaughan Thomson, long before 1840, described his discovery of a Schizopod which was brilliantly luminous. The third memoir of that author's zoological researches is entitled, "On the

<sup>1</sup> Om Slaegten Thysanopoda, og dens Norske Arter,' Christiania Vidensk Forh., 1863.

Luminosity of the Ocean, with descriptions of some remarkable species of Phosphorescent Animals, and particularly of the four new genera—Noctiluca, Cynthia, Lucifer, and Podopsis of the Schizopodæ.” In this memoir he relates how he captured the species he calls Noctiluca in the Atlantic, on his voyage home from the Mauritius, and says the animal gave out brilliant scintillations in the dark when disturbed. It was in most parts perfectly transparent, but turgid here and there, with orange-red pigment, particularly on its anterior feet.

Thomson identified his specimens with a form described by Sir Joseph Banks, and observed by him to be luminous, and to be the chief cause of the phosphorescence of the sea on a certain occasion. Banks gave the animal the name *Cancer fulgens*, which Thomson altered. The latter was quite unaware that the luminosity was due to and limited to special organs, and makes no mention of any “accessory eyes,” although there is little doubt that his Noctiluca (which has not yet been identified with one of the species now recognised) belonged to the family Euphausiidæ.

The naturalists on board the “Challenger” were familiar with the phosphorescence of the Euphausiidæ, and observed the connection between the emission of light and the organs known as accessory eyes.

Mr. John Murray paid particular attention to animal phosphorescence and to the captures of the tow-net, and therefore was repeatedly impressed with the brilliancy of the luminosity of members of this family, and its exclusive origin in the special organs.

The account given in the ‘Narrative of the Cruise of the “Challenger”’ (vol. i, p. 743) is as follows:

“The phosphorescent light emitted by the species of Euphausiidæ was frequently under observation during the cruise. If one of these be taken up by a pair of forceps when newly caught, a pair of bright phosphorescent spots will be observed directly behind the eyes, two other pairs on the trunk, and four other spots situated along the median line of the tail. These can all be quite well seen by the naked eye. The pair

close to the eyes are first and most brilliantly illuminated, and then the light, which is bluish white, spreads to the other organs on the trunk and tail. After a brilliant flash has been emitted from the organs they glow for some time with a dull light. The light is given out at will by the animal, and usually, but not always, when irritated. Subsequent flashes become less and less bright till the animal appears to lose the power of emitting light. If the organs be removed with the forceps the points will glow brightly for some time, and when the animal is dying the whole body is frequently illuminated by a diffused light. These phosphorescent organs appear under the microscope as pale red spots, with a central, clear, lenticular body. The phosphorescent light comes from the red pigment surrounding the lenticular space.

"In August, 1880, Mr. Murray observed at night on the surface of the sea in the Farøe Channel, large patches and long streaks of apparently milky-white water. The tow-nets caught in these immense numbers of *Nyctiphanes* (*Thysanopoda*) *norvegica*, M. Sars, and the peculiar appearance of the water seemed to be due to the diffused light emitted from the phosphorescent organs of this species."

Professor G. C. Sars mentions the light producing function of the organs in his "Preliminary Notices of the Schizopoda of the 'Challenger,'" published in 1883,<sup>1</sup> and in his "Report on the Schizopoda" (1885), he discusses at some length their structure and function in his account of the genus *Euphausia*. He believes, after careful examination of the structures both in spirit specimens and in the living animal, that they are highly differentiated luminous organs. It is unnecessary to repeat his description of the position of the organs, it confirms that already quoted from Claus, with the addition of the pair of organs situated in the eye peduncles and mentioned in the "Challenger" narrative. He says the organs are globular bodies with a very complicated structure, bearing in some particulars great resemblance to that of the eyes in Vertebrates. A rather thick and elastic cuticle forms the outer envelope of

<sup>1</sup> Christiania Videns. Selsk. Forh., 1883.



the organ, which, moreover, in fresh specimens is coated with a beautiful red pigment in its posterior half, whereas the front portion remains quite pellucid. On closer examination the two portions are found to fit as it were into each other without being actually connate. At the junction a glistening ring may be seen internally, encompassing in the middle a highly refractive lenticular corpuscle. The posterior hemisphere is filled up with cellular matter, in the midst of which lies embedded a flabelliform bunch of exceedingly delicate fibres, exhibiting in fresh specimens a most beautiful iridescent lustre. "To the equatorial zone of the organ, moreover, two or three thin muscles are attached, admitting to a certain extent of its being rolled to and fro."

Sars then refers to the observation of J. Vaughan Thompson<sup>1</sup> that these Crustacea are highly luminous at night, and states that he himself has observed their luminosity in the Norwegian species, doubtless principally in *Nyctiphanes norvegica* and he found that the animal was able by varying the movements of the organs to increase or diminish the light at will. He believed that the chief light-producing matter was the fibrous fascicle lying in the centre of the organ. "Even if the organ be crushed and this fascicle be extracted it still continues to give forth a comparatively strong phosphorescent light when seen in the dark." The lens he believes to act as a condensor for the light, and the pigment coating behind to prevent the light being radiated in all directions. He gives four reasons which show that the organs are not eyes; (1) that the nerve to the organs is very thin and does not give rise to any special retinal expansion; (2) that the structure of the posterior portion of the organ is not that of an eye; (3) that the position of the organs is ill adapted for vision, and (4) the presence of one of the organs in the eye peduncle.

He points out that the ocular organ is immobile, and entirely lacks the front hemisphere with its lens, and that the light from it is more intense and more steady than that from the others.

Professor Sars's description of the position of the organs

<sup>1</sup> Quoted by mistake as W. Thomson.

on the body leaves nothing to be added ; it is necessary here simply to indicate their position briefly. The organ in the eye peduncle is dorsal to and somewhat on the outer side of the eye, and in close contact with the latter. The thoracic organs are contained in the coxal segments of their respective limbs ; the anterior pair are on the internal side of the limb, and cannot be seen in the ordinary condition and position of the animal ; they are directed downward and inward when the animal is on its ventral surface. The posterior pair are on the external side of the limb, and are directed downward, outward, and backward. This pair are quite conspicuous in the living animal, and in the dead specimen without any operation being performed on it. The abdominal organs are simply directed downwards.

The position of the organs is constant throughout all the genera of Euphausiidae with two exceptions. In Stylocheiron there are only five, one ocular pair, the posterior thoracic pair, which have an additional lens, and a single caudal organ. In Benteuphausia, which is the only one brought up by the "Challenger" from deep water (1000—1800 fathoms), according to Sars there are no luminous organs and the eyes are imperfectly developed, while Willemoes Soehn believed that organs he found on each of the thoracic limbs were the luminous organs.

We have examined, at Mr. Murray's suggestion, the structure of the luminous organs, or as they may more conveniently be called, photospheria, of *Nyctiphanes norvegica*, G. O. Sars. Before proceeding to describe the result of our studies we will say a few words as to the distribution of the species. It is a distinctly northern form, being absent from the Mediterranean and the warmer parts of the Atlantic. It is abundant on the west coast of Norway, having, as we have already mentioned, been first defined from Norwegian specimens by M. Sars under the name *Thysanopoda norvegica*. But in considering the localities where specimens have been taken, it is necessary to mention whether the capture was made from the surface waters or from the bottom. The adult, so far as our information allows of a decision, lives on the bottom, and never

swims far from the ground, while the young, up to half or three quarters the size of the adult, occur abundantly at the very surface, and at all intermediate depths. As mentioned above, Mr. Murray found swarms of individuals at the surface in the Farøe Channel, but none of these were full grown, and very few more than half the adult size. Within the last two or three years the species has been recognised as common enough in the Clyde sea-area.

The place where we obtained it in abundance for the purpose of the examination described in this paper, was a deep area ninety to ninety-five fathoms from the surface, situated off Brodick Bay, and running north and south. We captured it in a shrimp trawl worked from the Steam Yacht "Medusa," of the Scottish Marine Station, and we took large numbers of living specimens to the small house-boat laboratory called the "Ark," stationed at Millport. Young specimens up to a quarter of an inch long were taken by Mr. now Professor J. R. Henderson in the Firth of Forth in 1884, and in June of the present year we captured a number of specimens of the same size at the surface by means of the tow-net, in the neighbourhood of St. Abb's Head. The eggs and larvæ have never been described, and, as far as we know, never captured. We are unable to state whether the adult exists anywhere in the Firth of Forth or its neighbourhood, or in the North Sea. As the young occur at the surface in the region of the Firth of Forth, it is natural to conclude that the adults occur at no great distance; but this inference requires verification. It is clear that the adult is pretty widely distributed in depths over, say, sixty fathoms off the north-western shores of Europe.

It is obvious from the preceding historical survey that no complete histological analysis of the structure of the photospheria in Euphausiidæ has yet been made. All the organs in our species, except the pair in the eye peduncles, have the same structure, and fig. 1 showing a vertical transverse section of the photospherion of the first abdominal segment in situ illustrates the following description: the section passes through

the principal axis of the organ. The posterior part of the organ is bounded by a layer composed of wavy fibres or laminae, which are generally parallel in direction, but are to some extent interlaced and anastomosed; this layer is of considerable thickness, and forms a hemispherical cup open in front, and in front only; it is perfectly continuous everywhere behind its free edge, being pierced by no apertures whatever. This is the layer called by Claus a coarse pigmented fibrous membrane, and by G. O. Sars a thick elastic cuticle. The layer is not pigmented except on its internal surface, which will be referred to later. It is non-cellular, that is, contains no nuclei nor distinguishable cell-areas. This layer resembles to some extent a tapetum, and as one of its functions is undoubtedly the reflection of light from its internal surface, we may adopt for it the name used for a similar layer in the phosphorescent organs of fishes by Von Lendenfeld, that of reflector. Covering the exterior surface of the reflector is a flat, mosaic-like epithelium of polygonal red pigment-cells. The appearance of these, as seen after slight compression in a fresh organ, is shown in fig. 2.

Red pigment is present in patches and dots in other parts of the animal's body, and is everywhere contained in stellate mesoblastic chromatophores, situated close beneath the epidermis. It is obvious that the epithelial covering of the reflector is a special development of these chromatophores. Where the chromatophores are not present the body of the animal during life is beautifully pellucid. Internal to the reflector is a layer of large cells, somewhat higher than broad, and each containing a large nucleus. These cells are, in some places, in two layers, though the layers are not regularly superimposed. The largest cells are near the surface of the reflector, and smaller ones exist above them in some parts. The internal surface of the cellular layer is perfectly smooth and hemispherical in shape, and in the hollow contained by it is a curious fibrillar mass. The fibrils of this mass are for the most part straight, and in its external part are perpendicular to the surface of the cellular layer, while the core of the mass



consists of straight fibrils in two bundles crossing at right angles, and other bundles in other directions. In front of the fibrillar mass are seen one or more flat cells which belong to the cellular layer. In front of these is the biconvex lens (*l.*, fig. 1), perfectly homogeneous in structure, and highly refringent; its diameter exceeds that of the fibrillar mass, so that it rests on the edges of the cellular layer. In front of the lens is a layer of cellular tissue, which contains a ring of circular fibres, running round the edge of the lens. The cells of this layer, which may be called a cornea, are much smaller and more regular than those of the posterior cellular layer. Between the fibrous ring and the posterior part of the organ, outside the lens, is a kind of cleft occupied by a few small cells, which separate the ring from the anterior edge of the reflector.

The red pigment of the cells coating the reflector disappears in spirit, and the peculiar colour of the internal surface of that layer cannot be seen in sections. The reflector and the fibrous ring absorb carmine very slightly, and the only deeply-stained parts of the sections are the cell nuclei. The organ is situated immediately below the epidermis (*ep.*, fig. 1), and connected with it by cellular strands, which, passing in at the cleft between the edge of the reflector and the fibrous ring, place the posterior cellular layer in structural continuity with the epidermis. It is possibly by this cellular communication that nervous impulses are conveyed to the organ. The organ is surrounded by a blood space (*lac.*, fig. 1), and the cellular strands cross this space. In the thoracic organs there are also thin bands of muscle passing across the space to be inserted in the surface of the organ, but we have not found such muscles connected with the abdominal organs. The subneural artery passes between each of the abdominal organs and the pair of nerve ganglia which lies close to it dorsally.

The structure of the photospherion of the ocular peduncle differs considerably from that of the rest. The difference consists in the absence of the lens, and of the cornea as a separate and distinct layer. The organ (fig. 3) is continuous with the

epidermis, from which it projects inwards in the form of a somewhat elongated knob. The principal axis of the organ is oblique to the external surface. The organ is placed immediately outside the tissues of the compound eye, a layer of dense pigment separating the reflector from the ocular elements, as is seen in fig. 3, representing a longitudinal section through the photospherion and part of the eye. The reflector is present, and has the same structure as in the other organs, but it extends nearer to the external surface, its free edge being immediately beneath the epidermis. As in the other organs, it is coated externally by a mosaic of polygonal red pigment-cells. Internal to the reflector is the posterior cellular layer, also having the same structure as in the other organs, but becoming at its edge continuous with the epidermis. Internal to the cellular layer is a layer of straight fibrils. This layer is of a uniform thickness, equal to that of the cellular layer, and it is limited internally by a hollow surface. The hollow is filled up by a mass, which is almost homogeneous at the base near the surface of the fibrillar layer, but passes by gradual transition into a layer of somewhat elongated cells, which themselves are continuous with the epidermis.

There is sometimes visible in the section a blood space between the exterior of the organ and the surrounding tissues, but we have never seen any muscles or cellular strands like those occurring in the other organs.

It is to be noted that, with the exception of the layer of straight fibrils and the reflector, every layer in the photospherion of the ocular peduncle is continuous with the epidermis. It seems a necessary inference from this that the organ is produced by differentiation of parts from a simple thickening of the epidermic layer of cells. The reflector is probably a specialisation of subepidermic mesoblastic tissue; the posterior cellular layer is a specialisation of the deepest portion of the epidermic thickening, and remains continuous with the epidermis at its free edge. Similarly, the central portion of the thickening is modified into the almost homogeneous mass filling the cavity enclosed by the layer of straight fibrils. This layer itself is

also, in all probability, produced by differentiation of other cells of the thickening.

It seems also clear that a few steps farther in the same process of molification would produce an organ exactly like the photospheria in the thorax and abdomen, and that we are justified in regarding the organ of the eye peduncle as permanently retaining a condition which in other organs is merely a stage of development. The more complicated structure of the other organs is probably derived from the condition seen in the ocular organ in the following manner:—The edges of the reflector are turned somewhat inwards; the layer of straight fibrils is compressed into a solid mass with slight modifications in the arrangement of the fibrils in the centre of this mass. The homogeneous mass in the hollow of the fibrillar layer in the ocular organ may be taken as representing the lens, which, when the fibrillar layer was compressed, would be removed farther outwards, and lie in front of the fibrillar mass. This supposition involves the view that the lens in the posterior organs is derived from the bodily conversion of cells, and not by extracellular secretion. But it may be a “cuticular” structure deposited by the cells in front of it. The cells which in the ocular organ lie between the fibrillar layer and the epidermis obviously only need to separate from the epidermis and form a distinct cap in order to become the cornea of the more complicated organ, while the fibrous ring at the base of the cornea seems to be produced by the transformation of some of the cells of the cornea, for in sections nuclei are often to be seen in the substance of the ring. The separation of the cornea would, of course, push the posterior part of the organ into a deeper position in the body, and separate the edges of the cellular layer to a great extent from the epidermis. We say to a great extent, for it is to be borne in mind that in the posterior complicated organs the cellular layer remains connected with the epidermis by cellular strands. It is probable that the nervous stimulation of the organ reaches it by these cellular strands.

We have not been able yet to follow out from the earliest

stage the actual development of the organs, and so test the above hypothetical account, but we have examined the condition of the posterior organs in very young specimens, which were only a quarter of an inch in length, but which were already similar in external characters to the adult. In these young specimens the organs already possess all the different parts present in the adult organs, but in a somewhat embryonic condition. A section of one of these organs is shown in fig. 5. It is from one of the anterior thoracic pair. It will be seen that the continuity of the cornea and of the posterior cell layer with the epidermis is well shown, and the whole organ is evidently arising by differentiation in an epidermic thickening. The fibrillar mass is different in appearance from that in the adult, the striations being all parallel to the principal axis of the organ. The cells of the posterior cell layer still retain their primitive character. Fig. 6 shows a similar section of the first abdominal organ at the same stage.

#### Function of the Organs.

Nearly everybody who has written about the luminosity of the Euphausiidæ has mentioned that the emission of light is intermittent, and is directly affected by stimulation. It is usually also stated that the activity of the photospheria is under the control of the will of the animal, and is soon exhausted by repeated exercise. Our observations go to confirm these statements, but we regret to say that they are not altogether conclusive, and it is desirable that experiments more rigidly exact should be made on the living animals. The observations are as follow:

The behaviour of the animals when alive, and, as far as can be judged after capture, in a healthy normal condition, is peculiar. They are in a state of almost incessant activity, swimming restlessly forwards and struggling vigorously against any obstacle they come into collision with. Their motion is due almost entirely to the limbs, the sudden backward movement produced by flexion of the abdomen is scarcely ever observed. And it is curious to note that they are as often on their dorsal



as on their ventral surface when swimming, or perhaps oftener in the latter position. This is of some importance in relation to the ventral position of the luminous organs. The contrast between the apparently excited, hurried, heedless motions of *Nyctiphanes*, and the graceful, wavy movement of *Mysis*, which is always either suspended in perfect balance with a regular motion of its limbs, or escaping by a swift, well-directed, backward dart, is very striking.

In total darkness the animals swimming about in a glass jar of sea-water gave out short flashes of light from time to time. Each flash was of short duration, but sometimes lasted longer than at others; when several animals gave out light simultaneously or in rapid succession, the effect was very brilliant and beautiful, but nothing like continuous luminosity was ever observed.

Handling.—When the hand was plunged in the water among the animals, any one of them when touched immediately gave forth a flash. When an animal was caught and removed from the water between the finger and thumb, all the organs emitted a brilliant light for five to ten seconds, while the creature was flapping its abdomen vigorously and trying to escape. Then followed an interrupted series of flashes lasting ten seconds more, and then the animal would become quiet and no light could be seen. But when slight pressure was administered, all the organs flashed again, the duration of the flash being longer when the pinch was stronger. When the animal was crushed between the fingers and the tissues rubbed between the hands, certain particles were luminous and remained continuously so until they were dry. When an organ was dissected out from the abdomen the light ceased, and by the time it was mounted and placed under the microscope all luminosity had vanished. But when the organ under the microscope was crushed the field was lit up and continued so for some time. When an eye-stalk was cut off by scissors the ocular organ became luminous for an instant when the division took place. After the animals had been in captivity twenty-four hours, they were by no means so easily excited to

give out light. Only about one in four became luminous on being removed from the water.

**Chemical Stimulation.**—When an animal was dropped into a saturated solution of bichloride of mercury all the organs shone most brilliantly from five to seven seconds, when the muscles were being violently exerted; in one case the light lasted for thirty seconds. A similar result followed immersion in nitric acid,  $\frac{1}{20}$  per cent., but death ensued more quickly. In both cases the posterior organs ceased to shine first, and the ocular organs were the last to be extinguished.

One of us spent nearly a whole day in the laboratory examining the fresh organs with the microscope in order to ascertain which part of the photospherion produced the light, and the results of this examination were afterwards verified by both of us. It was found, by repeated trials, that it was occasionally possible by crushing the organ under a cover-glass to separate all the component layers from one another. The red pigment was usually dispersed in the operation. All other parts of the organ were seen to be perfectly transparent, including the greater part of the thickness of the reflector, but excepting the internal surface of that layer. That surface in transmitted light glowed with a beautiful luminous-looking, rosy-purple colour, reminding one of a sunset tint. When the light from below was cut off and the preparation viewed by reflected light, the colour was changed to its complementary tint, namely, yellowish-green. The appearance lasted as long as the preparation remained moist, over half an hour, but as time went on the purple colour became more and more tinged with blue, and the complementary colour more distinctly yellow. The appearance of the most successful preparation is faintly indicated by fig. 7. The most striking fact about the matter was that when the light from the mirror was shut off, and the preparation viewed through a low power, illuminated only by diffused daylight, every part of the preparation was invisible except the coloured surface of the reflector, which appeared to give off a green light in a dark field. But when the daylight was entirely cut off by a cloth coat placed over the

microscope and the head of the observer the green colour disappeared, and nothing could be seen. It is evident then that the inner surface of the reflector possesses in a marked degree the property of fluorescence, and the appearance described is due to this property, not to a pigment. When white light falls upon the surface in question its more refrangible rays are made less refrangible and given off as a greenish light, while the purple colour seen by transmitted light is due to the absorption of the blue and green rays, and the transmission of the remainder.

As stated above it appeared from the examination under the microscope that the surface of the reflector gave off no light under the conditions described, in perfect darkness. But we afterwards found that when a slide containing a crushed organ was viewed by the naked eye in the dark there was always a luminous spot in the preparation, which shone with an intrinsic light, and on examination the luminous portion always proved to be the reflector, whose inner surface gave off the light. It is to be noted that the colour of the surface of the reflector was seen equally well, whether the surface was viewed directly or seen through the thickness of the reflector, for the latter was transparent.

It was stated above that when an animal was completely crushed by rubbing between the hands certain particles in the scattered tissues were continuously luminous in the dark. It was easy to pick up one of these particles with the forceps, place it on a slide and examine it with the microscope; this we did repeatedly, and always found that the particle was the whole or a portion of a reflector, which was always purple by transmitted light.

It is evident that our results differ from those of Sars with regard to this question of the light-producing part of the organ. We found no evidence whatever that the central mass of straight fibrils gave out light, and it never showed any colour phenomena: it was always transparent and colourless.

When the organs are examined in the living animal in daylight, the interior of each is seen to have a yellow-green

glistening sheen. This is doubtless due to the surface of the reflector, and is the same thing as the yellowish-green colour possessed by that surface in a crushed organ in reflected light under the microscope.

Unfortunately, the observation of the field of the microscope being lit up when a fresh organ was crushed beneath the objective in the dark, was not repeated after the above discoveries were made concerning the reflector; and, therefore, we cannot at present say what relation the above-described properties of the reflector have to the emission of flashes of light by the living animal. It is certain that these flashes are more intense than the continuous light given out by the reflector after the organ has been crushed. But the question which demands an answer is this: Is the sudden flash due to a sudden intensification of a phosphorescence always existing in the surface of the reflector? or is the sudden flash produced elsewhere (perhaps in the posterior cellular layer or in the central mass of fibrils), and the fluorescence of the reflector merely a property accessory to its principal function of reflecting the light so produced?

In attempting to understand the mechanism of the photospheria of the Euphausiidae it is natural to endeavour to get some enlightenment from a comparison between these and luminous organs in other animals. The best known luminous organs are those of the glowworm, and their structure and mechanism have been investigated by Max Schultze<sup>1</sup> and others. Schultze says that researches previous to his own have shown that oxygen is necessary to the emission of light, and that the intensity of light is under the control of the nervous system, while all attempts to isolate phosphorus from the organs have failed. He then proceeds to describe the structure of the organs, which consist of plates composed of two layers of cells. The deeper layer is opaque and non-luminous; its opacity is due to granules containing uric acid, and probably consisting of urate of ammonia, and the layer

<sup>1</sup> "Leuchtorgane von *Lampyrus splendidula*," 'Arch. f. mik. Anat.,' Bd. i, 1865.



acts merely as a reflector. The anterior layer is composed of pellucid polygonal cells, among which are numerous tracheæ whose ultimate ramifications end in stellate cells. Schultze found that the tracheal end-cells in the fresh condition reduced osmic acid very powerfully, and he concludes that they have a great affinity for oxygen, and that they are thus the principal agents in the production of the light, though the other cells of the layer are also luminous. At the same time he points out that tracheal end-cells occur in other organs besides the light organs, and wherever they occur powerfully reduce osmic acid. There is obviously at first sight very little agreement between the light organs of the glowworm and the photospheria of *Nyctiphanes*. If we compare the reflectors, we find that of the former, cellular; that of the latter, fibrous. Perhaps the posterior cellular layer of *Nyctiphanes* is similar to the superficial cellular layer in *Lampyrus*, but then we have not yet proved that the former is luminous.

We next have to compare the photospheria of *Nyctiphanes* with the luminous organs of fishes, which have been carefully and ably investigated by R. von Lendenfeld and Professor Moseley.<sup>1</sup> There is nothing in these organs of fishes which resembles the structure seen in *Nyctiphanes* at all closely. In the fish the phosphorescent organ usually contains structures of two kinds, a system of glandular tubes and a layer of superficial specialised epithelial cells. The glandular portion is always the deeper, the epithelial more superficial. Most of the organs have, in all probability, been developed in connection with the slime canal system. The nervous supply as a rule does not present any very striking peculiarity; there are certain large suborbital organs which are innervated by an enlarged branch of the trigeminus having a special lobe at its origin; the other organs are supplied by ordinary superficial nerves. There is usually an enveloping capsule with an internal reflect-

<sup>1</sup> 'Report on the Deep-Sea Fishes of the "Challenger," App. A; 'Report on the Structure of the Peculiar Organs in the Head of *Ipnotus*,' by Professor H. N. Moseley, F.R.S., App. B; 'Report on the Structure of the Phosphorescent Organs of Fishes,' by R. von Lendenfeld, Ph.D., F.Z.S.

ing surface, and this is morphologically a modified dermic scale. There is a special kind of cell often present which Lendenfeld regards as a specialised gland-cell. Each of these contains a highly refractive vesicle which represents the secretion of the gland-cell.

To take one or two examples. One of the most interesting of the organs described is that called "ocellar, regular, composite." Some of these are provided with a reflecting layer internal to the pigment, composed of calcareous spicules, and morphologically comparable to one or more scales. These organs are all formed on one general plan. There is a spherical deep portion surrounded externally by pigment, and continued towards the surface of the animal into a superficial portion, which is either a paraboloid or a parabola in some of its sections. The interior of the spherical portion is occupied by gland-tubes usually arranged radially, and lined by a single layer of gland-cells. Where the gland-tubes converge there is a space into which they pour their secretion. In the organs with reflectors cords composed of blood-vessels and nerves pierce the calcareous reflecting layer and extend vertically to the surface. These vertical columns are surrounded by radiating, slender cells, closely packed, so that each column of nerves and muscles forms the core of a cellular prism. Some of these slender cells are thin and inconspicuous, but among them are large club-shaped cells, which contain an oval, highly-refractive body, the latter apparently consisting of a cavity with a very fine wall, and containing fluid. The cellular prisms are separated from each other by a kind of packing composed of small cells, and the surface is also covered by layers of these cells. These organs are almost the only ones from which light has actually been observed to be emitted. Guppy<sup>1</sup> saw the light emitted from them in *Scopelus*. Lendenfeld thinks that the deeper gland-tubes pour out a slimy secretion into the distal portion, and that a mutual chemical action takes place between this slime and the typical phosphorescent clavate cells above mentioned, at the will of the fish,

<sup>1</sup> Ann. and Mag. Nat. Hist., ser. 5, vol. ix.

so that light is produced. This is not very clear. In another place he speaks of the secretion produced by glands in the lower part of an organ serving as a fuel, at the expense of which the slender cells above it may produce light. Again, in the case of the simple ocellar organs, he speaks of a special phosphorescent apparatus above, which produces light at the volition of the fish by using up or burning the secretion supplied by the gland, and stored in the space below.

These views, indefinite as they are, are yet inconsistent with anything that we know concerning animal physiology. It seems to me that they are of the same kind as the ancient notion that the heat of the body was due to the combustion of carbohydrates in the lungs by the oxygen taken in respiration. But that the emission of light is really dependent on oxidation in the luminous organs seems to have been conclusively proved in the case of the glowworm, in which the light was observed to disappear when the animal was placed in a medium destitute of oxygen. Lendenfeld regards the cellular layer at the back of the photospheria in Euphausiidæ as composed of gland-cells. I cannot see any particular reason for this, as I see no evidence of secretion being produced by them. At the same time it is probable enough that these cells are really the active agents in emitting light, the fluorescent surface of the stratified layer being only an accessory adjunct. All that can at present be said in the way of comparison is that the cells of this cellular layer in the Euphausiidæ are similar in general appearance to the cells of the luminous layer in *Lampyrus splendidula*, and that some or other of the cellular elements in the luminous organs of fishes are the active light-producing agents. With regard to the refractive globules in the club-shaped cells in fishes, it is possible that these really function as lenses, a number of lenses here perhaps being more advantageous than a single large lens, such as that of *Nyctiphanes*.

It is much to be desired that a careful investigation of the production of light in definite organs should be undertaken by a combination of physicists and physiologists, for hitherto the

most profound physical and physiological knowledge has not been applied to the problem. We content ourselves, in the above pages, with having worked out the internal structure of the organs of *Nyctiphanes* in detail, and having called attention to the interesting physical properties of the surface of the stratified layer.

P.S.—In the above brief review of researches on the phosphorescence of other animals than *Euphausiidae* we have omitted to refer to the important papers of Panceri. The principal of these are memoirs published by the Academy of Naples, namely, on the phosphorescence of the *Pennatulidae*, 1871, on that of *Pyrosoma* and *Pholas*, and on that of *Phylirrhæ*, 1872. Besides these there are valuable abstracts in the 'Comptes Rendus of the Acad. Roy. de Naples,' of the years 1871 and 1872. These abstracts are to be found in a French translation in the 'Ann d. Sci. Nat.,' tome xvi, 1872, and it is to this source that we owe our knowledge of Panceri's views.

The production of light in all the cases investigated by him is, according to Panceri, exclusively due to a special granular substance having apparently the nature and properties of a fat. He found a species of fish, *Trachypterus iris*, to be luminous in all parts; light emanated from almost the whole external surface, from the muscles when they were exposed, and from the viscera shortly after the abdominal cavity was opened. The liquid which drained from the flesh was luminous and gave that quality to every surface which it covered. This liquid was merely the oil of the animal, and the light was due to oxygen, being extinguished by carbonic acid and intensified by oxygen, not immediately but after an exposure of some hours.

In *Medusæ* Panceri found that the property of luminosity was confined to the epithelium either of the external or of internal surfaces, and was due to a substance contained in the cells of the epithelium, which substance resembled fat.

In *Pennatula* there are on each zooid eight cords or ridges on the external surface of the stomach. These ridges are composed principally of a substance of a fatty nature contained in



the cells of which the ridges consist. Light emanates exclusively from these ridges, and in the natural state of the *Pennatula* appears only in consequence of a stimulation; a single touch at any point of the colony may cause a luminous current, so to speak, to run through the whole. But the luminous matter can be caused to give out light after separation from the *Pennatula* by rubbing or by the application of fresh water.

In *Pyrosoma* there are two small luminous organs in each zooid near the external end of the branchial chamber. Each is composed of spherical cells and is attached to the inner surface of the outer layer of the integument. The cells contain a substance soluble in ether.

*Pholas* possesses several patches of excreting epithelium on the internal surface of the mantle; the cells of these patches give off a mucus which is in great part composed of fat and is luminous.

In *Phyllirrhoe* the cells which emit light are not superficial but are the ganglionic cells of the peripheral nervous system; but the light is due, not to the nervous matter properly speaking, but rather to a substance associated with the nervous matter, a substance which is soluble in alcohol and ether, and which gives out light when agitated even after the death of the animal.

It is evident then that there is no very clear connection between our observations and the views of Panceri. If, as the latter seems to think, the property of luminosity is always confined to a substance of a fatty nature, we cannot say in which part of the photospheria of *Nyctiphanes* the fatty substance occurs; we can only repeat that we saw light emitted only from the surface of the reflector.

## EXPLANATION OF PLATE XXIII,

Illustrating Messrs. Vallentin's and Cunningham's Memoir on  
"The Photospheria of Nyctiphanes Norvegica, G. O.  
Sars."

*List of Reference Letters.*

*ct.* Cuticle. *co.* Cornea. *ep.* Epidermis. *f.r.* Fibrous ring. *f.m.* Fibrillar mass. *ga.* Pair of ventral ganglia. *l.* Lens. *lac.* Blood lacuna. *p.c.* Posterior cellular layer. *re.* Reflector.

FIG. 1.—Section of the photospherion of the first abdominal somite *in situ*. The plane of the section is perpendicular to the principal axis of the animal's body, and passes through the principal axis of the organ.

FIG. 2.—External surface of the posterior thoracic photospherion, seen after slight compression in the fresh condition. (Zeiss A, oc. 2.)

FIG. 3.—Section of the photospherion of the ocular peduncle. The plane of the section passes through the principal axis of the organ.

FIG. 4.—Section of the photospherion of the ocular peduncle perpendicular to the principal axis of the organ.

FIG. 5.—Section of anterior thoracic photospherion from a young individual a quarter of an inch long.

FIG. 6.—Similar section of the organ of the first abdominal somite at the same stage.

FIG. 7.—Fresh preparation of a photospherion carefully crushed beneath the cover-glass. Transmitted light. (Zeiss C C, oc. 2.)



## On the Early Stages of the Development of a South American Species of Peripatus.

By

**W. L. Sclater, B.A., F.Z.S.**

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With Plate XXIV.

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### CONTENTS.

I. Introductory Remarks.	III. Details of the Development.
II. Structure of the Uterus.	IV. Conclusions.

### I. INTRODUCTORY REMARKS.

THE development of the South American form of *Peripatus* has been worked at by one author only, Kennel, who brought his material from Trinidad. In his two published papers (3) his results are so much at variance with the results arrived at by Mr. Sedgwick (6), who has worked solely at the South African form of the same genus, that it seems worth while to go through the early stages of the South American *Peripatus* again. This I have been enabled to do by means of specimens of *Peripatus* brought home by me alive from Demerara last winter, which have supplied me with a fairly complete series of embryos from the earliest stages onwards.

The species of *Peripatus* occurring in Demerara seems to me to differ materially from the other South American species, as I have pointed out in a note in the 'Proceedings of the Zoological Society' (5). But the absence of well-preserved material makes it very difficult to settle this question with any degree of certainty. Also it is to be hoped that Mr. Sedgwick, in a memoir which he is about to publish on the various species



of the genus *Peripatus*, will be able to clear up the difficulties of the subject.

It will be convenient, however, for me to distinguish the species now under investigation from those treated of by Kennel, and I propose, therefore, to allude to it as *Peripatus imthurni*, since it was Mr. E. F. im Thurn who first discovered *Peripatus* in British Guiana, and it was through his kindness and hospitality that I was enabled to procure my specimens. To Mr. Sedgwick also I owe very many thanks for all his kindness and help to me in my work on this subject. When I arrived in England it was he who preserved the specimens and their embryos, and afterwards helped me with many suggestions, besides allowing me to use all the many resources of his laboratory at Cambridge for the prosecution of my researches.

## II. STRUCTURE OF THE UTERUS.

When the uterus of *Peripatus* is examined it is found to consist of a long and very much coiled duct, which commences at the ovary as a slender tube, and, gradually widening, joins its fellow to form a short vagina, and opens to the exterior at the penultimate somite.

The uterus in the lower part is divided up by constrictions, the space between the constrictions being occupied by an embryo. Advancing towards the ovary the constrictions are longer and the swellings are smaller, till, for some distance from the ovary, the swellings entirely disappear. These swellings mark the position of the various embryos, and are usually eight to ten in number.

The position of the embryos is also marked by deposits of pigment, which appear as a pinky-red colour when seen in the solid uterus; these patches are found not at the actual position of the embryo itself but just in front and behind. In one or two instances, in the case of a very young embryo (*i.e.* the one nearest the ovary), the pigment was found to envelop it completely, so that it seems that the pigment is first formed all

round the embryo, and that it is then gradually divided into two patches, one in front, the other behind the embryo.

The most noticeable point about the uterus of *Peripatus* is that the contained embryos, which are from eight to ten in number, are all at different stages, the youngest near the ovary being perhaps in the segmentation stage, while the oldest will be completely formed and ready to be born.

All my specimens were collected at one season of the year (*i. e.* November and December), so I am unable to say whether they are pregnant all the year round, but it seems probable that this is the case. In this relation *Peripatus imthurni*, as also *P. torquatus* and *Edwardsii*, differ from the South African and New Zealand *Peripatus*, in which cases the development of the embryos, though going on all the year round, commences at one particular season, so that all the embryos found in the uterus of the female are approximately of one age. The structure of the uterus of *Peripatus* will be best seen by examining figs. 1 and 5.

Fig. 1 represents a longitudinal section through a piece of uterus not far removed from the ovary. At *e* is seen a young embryo lying in a cavity of the uterus, this cavity, which is the widened lumen of the uterus, is difficult to trace in front and behind, though in some places remnants of it can be detected; but on the whole it is generally obliterated.

The outer wall of the uterus is formed by a very slightly differentiated single layer of cells (*c.*), which though distinctly nucleated are without cell walls, so that they cannot be separated from one another very easily. Within this is the uterine epithelium, which simply consists of a mass of protoplasm in which is embedded a large number of nuclei. Slight traces of cell walls can be seen in fig. 5, which is a transverse section of a young embryo with its surrounding uterus. The inner line of the uterine epithelium is folded, so that it has a crinkled appearance (*ck.*); this is, doubtless, for the purpose of increasing the absorption surface, and it is by means of this crinkled appearance that the boundary between the uterus and embryo can be always detected. This folding of the inner layer

of the uterine epithelium is not seen very well in the longitudinal section (fig. 1), but it is better seen in fig. 5.

At either end of the embryo is seen a mass of pigment (*pg.*), in the form of black, star-shaped masses, which seem to block up the lumen of the uterus; around and near them are certain darkly-staining irregular masses of protoplasm (*x*), in which no structure whatever can be distinguished. Between the embryos is seen the very curious vacuolated tissue described by Kennel, of which it is very difficult to understand the meaning.

This tissue (*v. c.*) consists of at first a more irregular, afterwards of a more regular mass of vacuoles, separated from one another by thin lines of protoplasm which stain but slightly; along the outer border of these vacuoles there is a line of nuclei (*n.*) which are considerably larger than those of the ordinary uterine epithelium.

The appearance of this vacuolated tissue in transverse section is very well shown by Kennel (Part 1, Pl. VII, fig. 42).

The lines of protoplasm separating the vacuoles run straight from the central point of the section, where occasionally some remains of the lumen of the uterus can be seen, to the circumference where the vacuolated tissue comes in contact with the uterine epithelium. Just at this point, but in the vacuolated tissue, are found the numerous large nuclei generally arranged in a single row (*n.* in fig. 1).

This vacuolated tissue is never found near the embryo; where the embryo is present the vacuolated tissue is entirely replaced by the uterine epithelium, as is seen in fig. 1.

This vacuolated tissue is probably simply modified uterine epithelium, though how the change has been effected I am unable to suggest.

The explanation of this curious histological structure in the uterus of *P. imthurni* seems to me connected with the entire absence of yolk, and the small size of the ovum of this form. The difference in size between the youngest embryo (a sphere measuring .04 mm. in diameter) and the fully formed one, which is often an inch long, is enormous, and there must

be a very large quantity of food material absorbed in order to account for this increase in size. This food material must necessarily be derived from the uterine walls, and it appears to me that it is principally derived from these vacuolated regions, and that the pigment and the structureless protoplasm figured *x* are concerned in this phenomenon.

### III. DETAILS OF THE DEVELOPMENT.

The youngest embryos I have found are all of approximately the same age and are in the segmenting stage, but owing to their small size I have never been able to get them, except in a series of sections of unsplit uterus; and in this case the embryo is never so satisfactory, owing probably to the contraction of the uterine tissues due to the action of the reagents.

Fig. 2 represents what I take to be the youngest of all in the segmenting stages; it measures  $\cdot 04$  mm. across. It is not easy to assert definitely, but it probably contains eight nuclei embedded in a mass of unsegmented protoplasm, the whole lying free in the cavity of the uterus, which is always present where the embryo is, and for a short distance on either side of it.

In fig. 4, which represents an embryo ( $\cdot 07$  mm. in diameter) at a rather more advanced stage, the cells—or rather the nuclei, since there is as yet no sign of any cell partitions—have begun to arrange themselves in a ring round a central cavity. This embryo probably consists of twenty-four cells or rather nuclei. This embryo was also peculiar in that the uterus did not have the masses of pigment usually found in it on either side of the embryo. This embryo measures  $\cdot 08$  mm. long by  $\cdot 07$  mm. across.

Figs. 3 and 5 are approximately of the same age as fig. 4.

In fig. 5 the uterus has been drawn on one side to show the usual arrangement of the nuclei of the uterine epithelium; towards the embryo traces of cell outlines can be detected, but in the outer part of the uterine wall the uterus consists simply of a clear protoplasm with dark staining nuclei embedded in



it. The nuclei of the uterus stain much more darkly than the nuclei of the embryo itself.

In fig. 3 the only striking peculiarity is the presence of the two bodies (*p. b.*); it seems possible that these may be polar bodies, though beyond their appearance and position I have no further evidence to offer.

Kennel has also figured these early segmenting embryos, and my results do not differ materially from his; he has also figured what he believes to be polar bodies, but in no case do they seem to have separated from the embryo itself, but remain still buried in its substance.

The next stage, which is represented in fig. 6, presents a considerable difficulty; it seems to resemble in some respects fig. 51, Pl. viii, of Kennel.

This embryo ( $\cdot 105$  mm. in diameter), which at first I took to be a vesicle with the embryo inside, must, I think, be regarded as a stage previous to the one next to be described, i. e. the pseudogastrula stage.

The embryo consists of a single layer of cells marked out from one another only by their nuclei; it is approximately spherical. The nuclei on one side of the embryo, on being traced out, are found to form a small patch on that side of the sphere, and are considerably larger and more numerous, and it is at this spot, I take it, that invagination will take place.

That this embryo must be placed at this point in the series is evident from the size; as the embryos hitherto described varied from  $\cdot 04$  mm. to  $\cdot 08$  mm. in diameter, this one (i. e. fig. 4) is  $\cdot 105$  mm. in diameter and approximately spherical, while the pseudogastrula, to be described below, is  $\cdot 112$  mm. in diameter and  $\cdot 190$  mm. in length; this of course forms a fairly regular gradation of increase in size.

The ovum, therefore, of *Peripatus imthurni* is holoblastic, and the segmentation is fairly regular, the result being a blastosphere (fig. 6), that is, a hollow vesicle one cell thick. There is no sign of any attachment of the embryo to the wall of the uterus, and the inner wall of the uterus is marked by a thickened and crinkled line, which is very characteristic, and

which is very useful in later stages for determining the boundary between the embryo and the uterus. The size of the segmenting ova of *Peripatus imthurni* varies from .04 mm. to .07 mm. in diameter, and that of the blastosphere is .105 mm. in diameter.

The next stage, measuring .112 mm.  $\times$  .190 mm., represented in figures 7 A and 7 B, is a most important stage; during it the blastosphere, which was described above, is invaginated so as to form what appears to be a gastrula. I have several series of sections of embryos in this stage, but those figured, which are both from the same embryo, are by far the best; fig. 7 B is a transverse section through the embryo in the middle of its length, showing the invagination; fig. 7 A is a section through one end of the embryo beyond the point of invagination.

The cells are large and generally fairly well defined, more especially the outer layer; in the inner layer it is more difficult to distinguish cell-outlines; the nuclei of the outer layer show a distinct reticulum, and those of the inner layer are rather more chromophilous. The opening of the gastrula is situated on one side of the vesicle, that is, it opens at right to the long axis of the uterus.

This stage, which may be called the pseudogastrula stage, seems to me of great interest, and to be really the key of the whole matter.

The outer layer of the pseudogastrula forms in later stages the wall of the embryonic vesicle; the embryo proper is formed solely from the inner layer of the pseudogastrula.

Of the significance of this stage, and of its relations to the mammalian pseudogastrula, I will say more later on in the final part of the paper.

This stage doubtless corresponds to Kennel's stage, figured in Part I, Pl. viii, fig. 56, where he makes the outer wall of the gastrula *u. e.*, which he interpretes to be uterine epithelium; he also letters the point of invagination as *o.*, but neglects to give, as far as I can see, any explanation of *o.*

The result of this is that Kennel throughout his paper considers what I have termed the wall of the embryonic vesicle to

be part of the uterine epithelium and a purely uterine structure, whereas to me it seems evident that the wall of the embryonic vesicle has nothing whatever to do with the uterine epithelium, but is derived solely from the outer layer of the pseudogastrula exactly in the same way as the surrounding layer of the mammal's blastoderm, which afterwards forms the chorion, is derived from the outer cells of the Mammalian pseudogastrula.

From the pseudogastrula stage onward the embryo is always found lying in a hollow space, the embryonic vesicle, and attached on one side to the wall of the embryonic vesicle, which is formed from the outer layer of the pseudogastrula stage.

The embryo during this stage is at first sessile, afterwards a stalk is formed; and it is during the formation of the stalk that the two structures termed by Kennel amnion and placenta are found.

Figs. 8 and 11 represent the youngest embryos in vesicles which I have met with.

Fig 11 is drawn from an embryo lying in its vesicle still in the uterus, the uterus has been slightly split and the object drawn after being rendered transparent in benzole. The most noticeable point about fig. 11 is the enormous increase in size of the vesicle which is represented in the previous stage only by the slight split between the inner and outer layers of the pseudogastrula; the embryo, which is seen to form a small dark patch on one side of the vesicle, is oblong in shape and sessile. The size of the embryo is  $\cdot 16$  mm. long by  $\cdot 06$  mm. across; this is approximately of the same size as the embryo itself in the previous stage; but the vesicle in figure 11 measures  $\cdot 24$  mm. across as against  $\cdot 11$  mm. in the pseudogastrula stage (fig. 7 B).

Fig. 8 shows a section through an embryo measuring  $\cdot 084$  mm. in diameter with part of its vesicle of the same age as fig. 11. The wall of the vesicle consists of a band of clear protoplasm with definite nuclei at intervals. The embryo itself is composed of two parts, the basal part, in which the nuclei resemble those of the vesicle wall, and the embryo proper, consisting of large

cells in which cell outlines can only with great difficulty be distinguished.

These embryonic cells have a very peculiar appearance, due, as it seems, to the diffusion of the nuclear substance or chromatin throughout the cell substance; it therefore follows that no definite nucleus can be detected. Careful focussing, however, seems to indicate clear lines of protoplasm where no chromatin is present, and these lines of clear protoplasm seem themselves to demarcate the various cells of which the embryo is made up.

In the next stage the embryo is still sessile, that is, it is attached to the vesicle wall along its whole length.

Fig. 12 represents an embryo of about this stage, measuring about .1 mm. across, lying in its vesicle, the vesicle again lying in the cavity of the uterus; the two latter have been split open, so as to expose the embryo.

Figs. 9 A and 9 B represent two sections, an embryo and vesicle, of approximately the same size and age as fig. 12; the embryo .14 mm., the vesicle .28 mm. in diameter.

The vesicle wall (*v. w.*) is rather thicker in this stage, and the individual cells composing it are very much better defined than in the previous stages. The embryo proper consists, as before, of large cells with diffused chromatin and obscure cell outlines, and of supporting cells (*sp. c.*), whose nuclei stain very deeply, and whose cell outlines are invisible.

Between the two forms of cells of the embryo there has now appeared a cavity (*o*). This I believe to be arti-fact, and due to the action of reagents, especially as it is very inconstant in its appearance in embryos of this stage.

The only other noticeable feature of this stage is the so-called amnion (*am.*) of Kennel; this consists in the region of the embryo of a few scattered nuclei embedded in strings of protoplasm, in some cases surrounding and fusing with the embryo, in others fusing with the vesicle wall.

Fig. 9 B represents a section of the same vesicle behind the embryo proper. Here a complete ring of nucleated protoplasm is seen surrounding the space where farther forward would be



found the embryo. This is the highest development of the so-called amnion.

The amnion springs from the basal supporting cells of the embryo, as is asserted by Kennel.

This growth, which I have called an amnion, following Kennel's nomenclature, does not seem to me to fulfil the conditions of an amnion at all. An amnion may be described as a double fold of the non-embryonic area of a blastoderm (= vesicle wall), which is caused by the sinking of the heavy embryo into the cavity (= yolk-sac or vesicle) filled with fluid, the double folds finally fusing at the top.

This definition is true both for the amnion of the vertebrate and of the insect. In the case of *Peripatus* the outgrowth is not a double fold, but a single and thin string of protoplasm; it cannot possibly be explained by the mechanical descent of the embryo into the vesicle, since in that case the amnion would be formed on the other side of the embryo from folds in the vesicle wall.

It seems, therefore, that this so-called amnion of *Peripatus* has no sort of homology or analogy to the true amnion of insects and vertebrates. As to the use of this structure in *Peripatus*, it is at present impossible to dogmatize, but it seems to me that, like other embryonic organs, it has some part in the conveyance of nourishment to the embryo from the vesicle and uterus.

Another embryo—measuring the embryo .12 mm. the vesicle .25 mm. respectively—of about the same size and age as the one above described, is represented in fig. 10; it is remarkable for the thinness of the vesicle wall, which consists of a quite slender string of protoplasm with very few nuclei. This and several other examples which I have met with, of the same sort seem to show that the vesicle wall varies much in thickness at different times.

During the next stage the primary layers begin to form, and soon after that the legs begin to grow out, and the embryo begins to assume the form of the adult.

Figs. 13, 14A, and 14B represent whole embryos at this

stage. Figs. 14 A and 14 B are drawn from the same embryo, the latter by reflected light, and made transparent by benzole, the former by direct light in alcohol; fig. 13 is also drawn with reflected light.

Figs. 14 A and 14 B represent an acorn-shaped embryo corresponding to Kennel's fig. 12, lying in the unbroken embryonic vesicle; the band across the embryo and the shaded part of fig. 14 A, from which springs the stalk of the embryo from the thickened area of the vesicle wall, called by Kennel the placenta. The stalk, which is represented only in fig. 14 B, is drawn too slenderly; it should be considerably thicker.

The other embryo (fig. 13) resembles fig. 14 in every way, except that it has not been removed altogether from the uterus, of which the split half is still seen attached to the vesicle.

These embryos both measure .24 mm. across, and the vesicles are respectively .8 mm. and .6 mm. long.

When the embryo has got to this stage the layers begin to be differentiated. The mesoderm and endoderm are formed by a proliferation of cells which takes place at what will afterwards be the hind end of the embryo.

This process is illustrated in figs. 15 A, 15 B, and 15 C, which all represent sections from different parts of one embryo; fig. 15 A being at the hinder end and fig. 15 C towards the front end of the embryo. These figures show the embryo proper alone, neither stalk nor vesicle wall have been represented.

In fig. 15 A the embryo is seen to consist of a double layer of long-oval nuclei (*ec.*), from which are afterwards formed the ectoderm cells, and from which at one point (*pr.*) there is a proliferation of cells (*en.*) filling up the greater part of the cavity of the embryo; from these cells the endoderm and mesoderm are subsequently formed; the endoderm cells have a more granular and more rounded appearance than the ectoderm cells.

Fig. 15 B shows the appearance of the same embryo somewhat further forward; here all connection between the endoderm and ectoderm is lost, and the endoderm is growing

forward in the middle of the embryo at the expense of the proliferating cells behind.

In fig. 15 c, still farther in front, a cavity (*mes.*) begins to appear in the hitherto solid endoderm; this is the first commencement of the enteron.

Farther still in front the endoderm thins out somewhat, so as to form a narrow thin band encircling the enteron; still farther it gradually disappears, so that nothing is left at the extreme head end of the embryo but the ectoderm. From these proliferated cells the mesoderm is also formed later on. Another feature of this stage is the thickening of the ectoderm on one side, or rather, ventrally to form the nerve-cord. This is not marked at the hind end of the embryo, where the thickening extends all round, but is more marked at the front end (fig. 15 c), where on one side the ectoderm is seen to consist of a double layer (*n. c.*), on the other of only one; it is from part of this double layer that the nervous system will be subsequently formed.

The proliferation of cells takes place on the ventral side of the embryo distally to the stalk, which is attached to the dorsal side of the embryo at the head end. This proliferation, therefore, exactly corresponds to the primitive streak of *P. capensis* as described by Sedgwick; and all that has to be conceded is that in consequence of the extraordinary changes in the early stages due to the small size of the ovum and the absence of yolk, the blastopore of *P. capensis* described by Sedgwick has disappeared from *P. imthurni*, although its position is still marked by the primitive streak, which replaces the primitive streak + the blastopore of *P. capensis*.

After this stage I have not worked at the development of this form; for one reason I have not had time, for another because the later stages seem to me to resemble those of *P. Edwardsii* and *P. capensis* as arrived at by Kennel and Sedgwick respectively.

After a few words on the so-called placenta and amnion I will proceed to my conclusions.

The organ described by Kennel as a placenta does not

appear till somewhat later. I shall not call it a placenta, because it does not seem to me to bear any analogy to the mammalian placenta.

It seems to me that the best words to express the organs are the embryonic and vesicular thickening corresponding to the two parts of the placenta of Kennel (i. e. embryonic and uterine placentas).

An early stage in its development is shown in fig. 16, which represents part of the vesicle wall of a stage of the same age as fig. 15; here it is seen to consist of a large mass of cells (*pl.*) formed by the proliferation of the wall of the vesicle, which under ordinary circumstances consists of a single row of cells only. This is the vesicular thickening (= uterine part of the placenta) as distinguished from the embryonic thickening (= the embryonic placenta), which is merely the swollen part of the vesicle wall from which the stalk of attachment arises (*z.*).

The vesicular thickening is found in its fullest development rather towards the hinder end of the embryo, whereas the stalk of attachment and its swollen base are at the head end of the embryo.

The histological structure of the vesicular thickening at this stage is not remarkable; it consists of a mass of nucleated cells. The outlines of the cells are very apparent, and their protoplasm is in parts much vacuolated.

This stage corresponds in age to the embryo last described (fig. 15), and is the earliest stage at which the vesicle swelling is of any great size or importance.

Fig. 17 shows a much further development of the vesicular thickening; owing to its large size only a small portion of the vesicle wall (*v. w.*) is represented.

The histological structure of the vesicular thickening has here completely changed, all traces of cell walls have disappeared, the nuclei are darker and more distinct, and the protoplasm presents a very peculiar granular appearance which I have not seen elsewhere.

The vesicular thickening seems to be fused to the uterus wall itself, but of this I am not certain, since in all my sections the



uterus wall has been in each case separated from the vesicle wall, and on opening the fresh uterus the vesicle always comes away by itself.

The meaning of the cells marked *f* in fig. 17 has puzzled me; I think it highly probable that these nuclei and their adjacent protoplasm are food material for the embryo lying in the vesicle (not shown in the fig.), since the nuclei resemble nuclei found in the embryo, and the mass of cells, if followed through adjacent sections, are found to form a patch or cap of cells lying on the vesicular thickening; the vesicular thickening itself is seen when followed out to be directly continuous with the vesicle wall, so that the theory that the patch of cells (*f*) is merely a continuation of the vesicle wall, and the vesicular thickening (*pl.*) a product of the uterine epithelium, seems to me untenable.

This vesicle swelling persists till quite the end of the uterine life of the embryo as a thickening at the hinder end of the embryonic vesicle.

The placenta in the case of mammals is a vascular plexus formed by the uterine epithelium, which is in connection with a vascular plexus formed by part of the embryonic membranes.

In the case of *Peripatus imthurni* there is certainly, as far as I have been able to observe, no plexus of blood-vessels at all; and Kennel, I think, makes no mention of this matter.

But apart from that, since it may be argued that the word placenta can be applied to any uterine nourishing organ, whether vascular or non-vascular, the swelling of *Peripatus* is altogether an embryonic organ, the uterus takes no part in its formation whatever.

The vesicular thickening of *Peripatus* is formed entirely by the proliferation of the cells of the wall of the embryonic vesicle, which vesicle is originally derived from the outer wall of what I have called the pseudogastrula, so that it has nothing whatever to do with the wall of the uterus.

## IV. CONCLUSIONS.

On comparing the early stages of *Peripatus imthurni* as described above with the early stages of *P. capensis*, of which we now have a very complete account by Mr. Sedgwick (6), there will be seen to be an extraordinary discrepancy between the two forms.

Apart from the South American forms *P. Edwardsii* and *P. torquatus*, which resemble very closely in their anatomy and development *P. imthurni*, there is yet one more form, *P. novæ-zealandiæ*, about which a little is known through the researches of Moseley (4), Hutton (2), and Sedgwick (6), and at the development of which Miss Sheldon, of Cambridge, is now working.

A continuous series is made by the size of the ova of these three forms.

In *P. novæ-zealandiæ* the ovum measures 1.5 mm. long by 1.0 mm. across; the ovum consists almost entirely of a mass of yolk, and the segmentation is meroblastic.

In *P. capensis* the ovum is smaller, measuring only .17 mm., and though there is no yolk and the segmentation is total,<sup>1</sup> yet the spongy nature of the ovum, which consists of a very loose meshwork of protoplasm, clearly shows that the ovum has in this case only recently lost its yolk, and that with the loss of yolk a gradual reduction of its size is taking place.

In *P. imthurni* (as also in *P. torquatus* and *P. Edwardsii*, as shown by Kennel) the ovum is still smaller; Kennel gives the size of the ovum of *P. Edwardsii* as .04 mm., and this is also the diameter of my youngest embryo, which I believe to consist of about eight segmentation spheres; I have not met with any fully ripe ova among my sections, but I imagine that the embryo does not increase much in size during the early stages of segmentation.

In these forms the segmentation, as shown above, is complete, and there is no appearance of sponginess such as described by

<sup>1</sup> Sedgwick, on page 517 of the third part of his paper, would prefer to term the segmentation of *P. capensis* meroblastic.

Sedgwick in *P. capensis*; nor would one suspect, from the nature and size of the ovum, that it had been derived from a meroblastic ovum, and had only comparatively recently lost its yolk.

The only other instance of a holoblastic and alecithal ovum which has been derived from a meroblastic and telolecithal ovum, of which we have any knowledge, is the ovum of the placental mammals which has doubtless passed through a meroblastic and telolecithal stage such as is now presented by the ovum of *Ornithorhynchus*, our knowledge of which is due to Caldwell.

The results on the mammalian ovum of the loss of yolk are (1) a large diminution of the size of the ovum; (2) total segmentation; (3) the formation of a blastodermic vesicle which corresponds to the yolk-sac of meroblastic forms, the embryo proper being formed from only a small portion of the original mass of segmentation spheres which is attached to one side of the blastodermic vesicle.

Now, it seems to me that the loss of yolk has had precisely the same effect on the ovum of *Peripatus* that it has on the ovum of placental mammals, i. e. (1) diminution of the size of the ovum; (2) total segmentation, and (3) the formation of what I have termed the embryonic vesicle, which appears to me to be exactly analogous to the blastodermic vesicle of mammals.

The ovum of *Peripatus* has a stage directly comparable to the gastrula and blastopore stage of Van Beneden, by means of which the embryonic mass proper is separated from those cells which form the wall of the embryonic vesicle, and it is because this stage in *Peripatus*, as in the mammal, has nothing to do with the true gastrula and blastopore, such as is found in *Amphioxus*, that I have termed it the pseudogastrula stage.

It seems to me that this point is one which has never been sufficiently dwelt upon in morphology, namely, that like results may be due to the same mechanical cause,<sup>1</sup> and that it is not

<sup>1</sup> Professor Lankester some years ago ('Ann. and Mag. of Nat. Hist.' 1870) discussed this point and applied the terms "homoplasy" and "homoplastic" to such resemblances as distinguished from those due to heredity for which he proposed the terms "homogeny" and "homogenetic."

therefore necessary to suppose that because a certain process is brought about in the same way in two dissimilar forms, that there must be some genetic connection between these two forms. For instance, the same mechanical cause (i. e. loss of yolk) has brought about remarkably similar results in two entirely different groups of animals (i. e. mammals and *Peripatus*).

A point in the development of *Peripatus imthurni*, to which I have not yet alluded, and which I am unable to explain satisfactorily, is what may be termed the inversion of the layers.

An inspection of the figures will at once show that the epidermis of the young *Peripatus* is apparently formed from the inner layer of cells, and conversely, that the hypoblast is formed from the cells that are, morphologically speaking, part of the outside layer of the embryo. I have not been able to find an explanation of this inversion, though I have made great efforts to do so. I think, perhaps, that the so-called amnion may be concerned in its explanation; until, however, I am able to procure more material, I cannot offer any definite explanation of this curious phenomenon.

It may be interesting to note the differences between the adult *Peripati*, since they differ so immensely in their development.

The species of *Peripatus* about whose anatomy anything is known seem to fall into three groups:

(1) The New Zealand species (*P. NOVÆ-ZEALANDIÆ*), which stands by itself.

(2) The Cape species, three in number (*P. CAPENSIS*, *P. BREVIS*, and *P. BALFOURI*).

(3) The South American species (*P. EDWARDSII*, *P. TORQUATUS*, and *P. IMTHURNI*).

The only really important anatomical difference between the groups 2 and 3 is that in the South American species there is present between the ovary and the receptaculum seminis another closed thin-walled vesicle ("ovarian funnel" of Gaffron (1), receptaculum ovorum, Kennel (3)), which Sedgwick



regards as homologous with the nephridial funnel of the genital segment and its vesicle. This structure is entirely absent in the Cape species of *Peripatus*.

Also in the South American species the generative opening lies between a pair of well-developed legs, while in the Cape species the legs of the generative segment are rudimentary or represented only by the anal papillæ.

In the New Zealand species the legs of the generative segment are well developed, but the question of the presence or absence of the receptaculum ovarum does not seem to be quite settled.

These are the only really important anatomical differences between the three groups of *Peripatus* as far as is at present known.

The only other instance of such great variation in development between such nearly allied forms which I can call to memory is that of Bateson's *Balanoglossus*, which in its development differs largely from the ordinary *Tornaria balanoglossus*.

This, however, is easily explained by the difference of the habits of the two forms; Bateson's larva is a mud-living animal, while *Tornaria* is pelagic.

The curious thing about *Peripatus* is that, as far as is known, its habits and mode of life are much the same all over the world, so that the striking differences in the development of the three forms cannot be explained by change of habits modified by external conditions.

In conclusion, I wish to apologise to my readers for the incompleteness of my work, and for my uncertainty on many important points; my excuse is the want of time and the absence of material, since a portion of that which I brought from Demerara was not satisfactory. And as it seemed unlikely that for some time at least anyone would be able to procure more material, either alive or with the uterus adequately preserved, I have thought it better to publish the small contribution that I have been able to make towards our better knowledge of that most ancient and interesting of all living Arthropods—*Peripatus*.

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- (6) SEDGWICK, A.—"The Development of the Cape Species of *Peripatus*." Part I, with pls. xxxi, xxxii, 'Quart. Journ. Micr. Sci.,' xxv, pp. 446—449, 1885; Part II, with pls. xii—xiv, 'Quart. Journ. Micr. Sci.,' xxvi, pp. 175—212, 1886; Part III, with pls. xxxiv—xxxvii, 'Quart. Journ. Micr. Sci.,' xxvii, pp. 467—550, 1887.

## EXPLANATION OF PLATE XXIV

Illustrating Mr. W. L. Sclater's Memoir, "On the Early Stages of the Development of the South American Species of *Peripatus*."

*Complete List of Reference Letters.*

*am.* So-called amnion. *c.* Cuticular layer. *ck.* Folded inner edge of the uterine epithelium. *e.* Embryo proper. *ec.* Ectoderm. *en.* Endoderm. *f.* Cells of doubtful function, probably nourishing. *mes.* Mesenteron. *n.* Nuclei of vacuolated epithelium. *n.c.* Nerve-cord. *o.* Artificial cavity due to reagents. *p.b.* Polar body. *pg.* Pigment. *pl.* Vesicle swelling (placenta). *pr.* Primitive streak. *sp.c.* Supporting cells. *u.e.* Uterine epithelium. *ut.* Uterus. *v.* Vesicle. *v.e.* Vacuolated epithelium. *v.w.* Vesicle wall. *z.* Embryonic swelling (embryonic placenta) whence the stalk arises.

All the figures, except Figs. 1 and 11 to 13, are drawn with Zeiss's camera (obj. D, oc. 2), but Figs. 16 and 17 have been reduced to one half the original size.

FIG. 1.—Longitudinal section through the upper part of the uterus, showing a young embryo and the curious histological structure of the uterus. Drawn with Zeiss's camera. (Obj. A, oc. 2.)

FIG. 2.—Youngest embryo met with, measuring .04 mm. in diameter. It seems to consist of eight nuclei with surrounding protoplasm.

FIG. 3.—Embryo segmenting rather more advanced with polar bodies.

FIG. 4.—Embryo with commencing central cavity.

FIG. 5.—Segmenting embryo drawn with the surrounding uterus to show the structure of the uterus and its relation to the embryo.

FIG. 6.—Young blastosphere stage before gastrulation and after the completion of the segmentation.

FIGS. 7A and 7B.—Two sections of an embryo in the pseudogastrula stage. Fig. 7A shows the condition of the embryo at one end beyond the influence of the invagination; Fig. 7B is a transverse section through the gastrula and its blastopore.

FIG. 8.—Youngest embryo found in a vesicle. The wall of the vesicle is much broken, only a very small part being represented in the figure.

FIGS. 9A and 9B.—Two sections through a vesicle and embryo of moderate size. The embryo is still sessile. Fig. 9A represents a section through the middle of the embryo, and shows the so-called amnion in part and the sup-

porting cells (*sp. c.*); Fig. 9B is cut through the vesicle behind the region of the embryo, and shows the amnion at its highest development.

FIG. 10.—Section through an embryo of almost the same age as Fig. 9, probably a little older. The vesicle wall in this case is reduced to a very thin string of protoplasm with a few nuclei embedded in it.

FIGS. 11, 12, 13, 14A and 14B are drawings of solid embryos; in the case of Figs. 11, 12, and 13, lying in the uterus, which has been split open to expose them; in the case of Figs. 14A and 14B the embryo has been removed from the uterus. All, with the exception of Fig. 14A, have been drawn with a Zeiss A after being made transparent by soaking in benzole. Fig. 14A was drawn when lying in absolute alcohol by refracted light.

Fig. 11. Stage about the same age as Fig. 8. The embryo is entirely sessile; there is no sign of a stalk. The embryo measures .16 mm.  $\times$  .06 mm.

Fig. 12. Stage of about the same age as Figs. 9A and 9B. The embryo is shown lying in the vesicle, which is in turn shown lying in the uterus; both uterus and vesicle having been split open.

Fig. 13. A stalked embryo in a vesicle, the vesicle lying in the split uterus. Embryo measures .24 mm. long.

FIGS. 14A and 14B. The same embryo, drawn, the former by refracted, the latter by reflected, light; Fig. 14A a ventral view, Fig. 14B a side view; show a vesicle with an acorn-shaped embryo lying within it. The embryo is stalked, the stalk springing from the darker area (so-called embryonic placenta). The embryo measures about .24 mm. across.

FIGS. 15A, 15B, and 15C.—Three sections through different parts of the same embryo. Fig. 15A is the posterior of the three, Fig. 15B the middle one, and Fig. 15C the most anterior. Fig. 15A shows the primitive streak (*pr.*), Fig. 15B the clump of cells growing forward from that point, Fig. 15C the commencing mesenteron.

FIG. 16.—Part of the vesicle wall of an embryo of the same age as Fig. 15, showing the commencement of the formation of the so-called placenta.

FIG. 17.—Later stage in the development of the placenta.





## On the Anatomy of *Allurus tetraedrus* (Eisen).

By

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With Plate XXV.

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*Allurus* was first recognised as a distinct genus by Eisen,<sup>1</sup> who described the worm from specimens found in Sweden. It has since been recorded by Dr. Rosa,<sup>2</sup> from Northern Italy; as it is probably identical with Hoffmeister's<sup>3</sup> *Lumbricus agilis*, it occurs also in North Germany and in Great Britain and France.

The specimen described in the present paper comes from the island of Tenerife. I received it alive with a number of other specimens of *Lumbricus* and *Allolobophora* from the Rev. C. V. Goddard, who was good enough, at the request of Mr. Stogdon, of Harrow, to furnish me with a sample of the earth-worm fauna of Tenerife.

The papers already referred to contain no account of the internal anatomy of *Allurus*, and I am not aware that we at present possess any knowledge of its structure.

I have thought it worth while, therefore, to publish the following notes.

With regard to external characters, I have little to add to

<sup>1</sup> 'Öfv. af Kongl. Vetensk. Akad. Förh.,' 1870, p. 966.

<sup>2</sup> 'I. Lumbricidi del Piemonte,' p. 51.

<sup>3</sup> 'Die bis jetzt bekannten Arten aus der Familie der Regenwürmer,' p. 36.

the descriptions of Rosa and others. In every particular my specimen agreed with the descriptions given by those authors. The first dorsal pore lies between segments 4 and 5, opening of course into the latter segment.<sup>1</sup> The most important point mentioned hitherto among the external characters of *Allurus* is the forward position of the male reproductive apertures and the clitellum; the former are upon the 13th segment, the latter extends from Segments 22—27.

**Anatomy.**—The single specimen at my disposal was carefully prepared for histological purposes; the anterior region was investigated by means of longitudinal sections; the clitellar region was studied by a continuous series of transverse sections.

**Reproductive Organs.**—The testes are two pairs (Pl. XXV, fig. 2 *t*); they are situated on the anterior mesentery of Segments 10 and 11; they correspond, therefore, in number and position as well as in structure to the testes of *Lumbricus* and many other genera.

The seminal reservoirs (fig. 2 *v. s.*) occupy Segments 9, 10, 11, and 12. The two anterior pairs are smaller than the two posterior, and are attached to the hinder septum of their segment; the posterior pairs of seminal reservoirs are attached to the anterior wall of their segment.

The disposition of the vesiculæ is, in fact, precisely that of *Allolobophora*<sup>2</sup> and of *Criodrilus*;<sup>3</sup> as in those genera the funnels of the vasa deferentia float freely in their segments (10 and 11), and are not in any way enclosed by the seminal reservoirs.

The vasa deferentia unite in the 11th segment to form a single tube with the usual structure, which opens on to the exterior in Segment 13. The termination of the vas deferens is stated by Rosa to be furnished with an atrium, confined to the 13th segment. The body which Rosa terms an "atrium" does not appear to me to be really comparable to an atrium;

<sup>1</sup> 'Ude ('Zeitschr. f. wiss. Zool.,' 1885, p. 139) states that the first dorsal pore is between 3 and 4.

<sup>2</sup> Bergh, 'Zeitsch. f. wiss. Zool.,' 1886, p. 314.

<sup>3</sup> Benham, this Journal, 1887, p. 567.

it is formed by a mass of glandular cells, exactly like those of the clitellum, which form a rounded mass (see fig. 5) through which the vas deferens passes without losing its distinctness; there is no cavity into which the vas deferens opens. It appears to resemble in every way a similar structure in *Criodrilus*, which Benham<sup>1</sup> has more correctly spoken of as "prostate."

Rosa's account of the organ in question differs from that of Benham. My own observations indirectly confirm the description given by Benham.

In *Allurus* the clitellum does not commence until the 22nd segment, whereas in *Criodrilus* it begins in the 15th segment; the "prostate" gland has, however, the same minute structure as the clitellum, and has every appearance of being a solid ingrowth of the epidermis. In the succeeding segments, including those of the clitellum, there is (fig. 8) a solid ridge of glandular cells on each side of the body, just above the ventral pair of setæ; this ridge is continuous in front with the "prostate" glands, and consists of a mass of cells exactly like those of the prostate; it is plainly connected, as shown in the figure cited, with the epidermis.

The ovaries<sup>2</sup> (figs. 2, 5, *ov.*) are in Segment 13, and occupy the usual position.

The oviducts (figs. 2, 5, *od.*) open by a much plicated funnel into the same segment; their external aperture is in Segment 14 (fig. 1, ♀).

A receptaculum ovarum (figs. 2, 5, *ro.*) is present in Segment 14. Its cavity is continuous with the oviducal funnel, through the disappearance of part of the septum.

The oviduct, therefore, opens on to the exterior of the body behind the male reproductive pores, as also occurs in *Rhynchelmis* and other *Lumbriculidæ*; this arrangement is not met with in any other earthworm, except *Moniligaster*.<sup>3</sup>

<sup>1</sup> Loc. cit., p. 568.

<sup>2</sup> My specimen possessed an additional pair of ovaries in Segment 14. This may or may not be an abnormal condition.

<sup>3</sup> Horst, 'Notes from the Leyden Museum,' 1887.

<sup>4</sup> Beddard, 'Ann. and Mag. Nat. Hist.,' Feb., 1886.



**Spermathecæ.**—I examined my sections for a long time without finding any evidence of the presence of spermathecæ. Finally, I succeeded in discovering in the 8th segment a structure which is illustrated in fig. 4; this consists of a minute pouch (*c.p.*), lined with epidermic cells, and plainly formed as an invagination of the epidermis, with which it is continuous. This pouch would not, however, have been seen in a dissection of the animal, because it only extends for a little way into the thickness of the muscular layers of the body wall. I am disposed to believe that it does represent a spermatheca, though presumably in a very immature condition. This presumption is strengthened by the fact that one at least of the ventral pair of setæ, near to which the pouch opens, is different in form from the other setæ of the body, being thinner and longer (fig. 3 *a*). I found no traces of spermathecæ in any but the 8th segment. Without assuming that there is only a single pair of spermathecæ present in the adult *Allurus*, I may point out that the position of these organs—situated in front of the testes, vasa deferentia funnels, and seminal reservoirs—is only found in such Lumbricidæ as *Allolobophora complanata* where there are a large number of pairs of these organs; furthermore, it is important to note that they do not in *Allurus* open on to the intersegmental furrow, but in the middle of the segment to one side of the setæ.

The alimentary tract presents no features of special interest. The gizzard is placed at the junction of the œsophagus and the intestine, as in the Lumbricidæ, and is preceded by a crop. It differs, however, from that of *Lumbricus* in only occupying a single segment, the 17th. Its structure, as shown in longitudinal section, is illustrated in fig. 9. At present there are no materials for a comparison of the minute structure of the gizzard in different forms. I give the figure because it is unlike any figure contained in Claparède's 'Mémorial' on the Histology of the Earthworm,<sup>1</sup> and also because it does not agree with preparations of

<sup>1</sup> 'Zeitschr. f. wiss. Zool.,' 1869.

my own of the gizzard of *Urochæta*. The intestine has a typhlosole.

The buccal cavity (see fig. 10) occupies the first three segments. The pharynx lies in 4, 5, and 6.

The œsophagus, from the middle of Segment 10 to the end of Segment 14, is furnished with a structure which corresponds with the calciferous glands of *Lumbricus* and other earth-worms; the œsophagus is here rather wide, and the lateral region is much folded; these longitudinal folds (fig. 2 *ca*) are quite continuous from segment to segment; there is no question of any separation into distinct glands. This arrangement is possibly to be regarded as a primitive one.

The epithelium of the œsophagus, which differs in character from that which covers the lateral folds, is very distinctly ciliated in the segment where the folds are developed (fig. 2 *a*).

In segment 10, at the junction of the anterior section of the œsophagus with that part which has just been described, is a short diverticulum on either side; this diverticulum marks off the non-ciliated anterior region of the œsophagus, which also differs from the ciliated region in the shape of its cells. They are not quite so tall and narrow as the ciliated cells. In all these particulars the diverticulum agrees in structure with the anterior section of the œsophagus.

The crop occupies the 15th and 16th segments.

With regard to the nervous system, I may mention that the cerebral ganglia are in the 4th segment (fig. 10), and that the ventral nerve-cord has cells along its whole length.

Nephridia.—These organs consist for the most part, as in the *Oligochæta* generally, of a series of "drain-pipe" cells; as in *Lumbricus* and other genera, the calibre of the inter-cellular duct, and of the cell which contains it, is at first less than it becomes afterwards. Fig. 11 is a transverse section through a nephridium which illustrates this fact; *a* are the smaller drain-pipe cells, *n* the larger. The nephridium is surrounded by a number of peritoneal cells (*p*.); these are oval in form, the protoplasm appearing almost homogeneous and have a darkly staining nucleus. The larger drain-pipe cells *n'* appear

to be embedded in the substance of other cells (*n*, fig. 11); these latter stain very slightly with borax-carminé, and the protoplasm is arranged in a reticulate fashion. The nucleus of the cell is small but conspicuous in that it is deeply stained; it is perfectly plain, as also shown in a longitudinal section (fig. 12) that the drain-pipe cells actually perforate these cells.

I cannot, however, be perfectly certain as to the correctness of the above description; it may be that the larger cells are simply specialised into a denser area surrounding the lumen, and a less darkly staining region situated peripherally. There is, however, a very sharply-marked boundary line between the two regions.

If the supposition that these two regions are really distinct cells, be correct, there is an obvious resemblance to *Clepsine*.<sup>1</sup>

#### Summary of structural differences from *Lumbricus* and *Allolobophora*.

(1) Position of male reproductive folds upon Segment 13 and therefore in front of female generative orifice (fig. 2).

(2) Presence of a single (?) pair of spermathecae opening on to the middle of their segment a little to one side of seta (fig. 4).

(3) Calciferous glands of consecutive segments not distinct from each other, occupying Segments 10—14.

(4) Gizzard confined to a single segment (No. 17).

(5) Structure of nephridia (figs. 11 and 12).

(6) The presence of a continuous glandular fold on either side of the body of the same structure as the clitellum, extending from the 4th to the 24th segment, and interrupting the muscular layers (figs. 2 and 8).

(7) The special development of this glandular mass in Segment 13, round the orifice of the vas deferens (fig. 5).

<sup>1</sup> A. G. Bourne, this Journal, 1885, p. 482.

## EXPLANATION OF PLATE XXV,

Illustrating Mr. Frank E. Beddard's paper "On the Anatomy of *Allurus tetraedrus*, Eisen."

FIG. 1.—*Allurus* sp., lateral view of anterior segments. ♀ oviducal pore. ♂. Pore of vas deferens. *sp.* Spermathecal pore. *d.* Clitellum. *n.* Nephridiopores.

FIG. 2.—Dissection of genital region of one side of the body. *v. s.* Seminal reservoirs. *t.* Testes. *v. d.* Funnels of vasa deferentia. *ov.* Ovary. *od.* Oviduct. *r. o.* Receptaculum ovarum. *ca.* Calciferous glands. *p.* Glandular fold of integument.

FIG. 3.—Elongated seta (*a*) from Segment 8 compared with one of the ordinary setæ (*b*).

FIG. 4.—Section through body wall of 8th Segment, to show the rudimentary spermatheca (*c. p.*).

FIG. 5.—Section through part of Segment 13. *v. d.* Vas deferens. *cl.* Mass of glandular cells. *ov.* Ovary. *od.* Oviduct. *r. o.* Receptaculum ovarum.

FIGS. 6 and 7.—Isolated glandular cells from region marked *cl.* in last figure.

FIG. 8.—Part of a transverse section through one of clitellar segments. *s.* Setæ of ventral pair. *n.* Nephridium, showing external aperture. *p.* Mass of glandular tissue.

FIG. 9.—Longitudinal section through gizzard. *m.* Longitudinal muscles. *t.* Transverse muscles. *e.* Epithelium. *c.* Internal cuticular lining. *bl.* These spaces were in many sections filled with blood.

FIG. 2 *a.*—Transverse section through œsophagus and calciferous glands.

FIG. 10.—Longitudinal section (diagrammatic) through anterior segments, to show position of cerebral ganglia. *b.* Buccal cavity. *ph.* Pharynx.

FIG. 11.—Transverse section through nephridial tubule. *p.* Peritoneal cells. *n'.* Drain-pipe cell, perforating, *n.*, another cell.

FIG. 12.—Longitudinal section, similar to preceding.





## The Development of the Cape Species of Peripatus.

### PART IV.

#### THE CHANGES FROM STAGE G TO BIRTH.

By

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With Plates XXVI, XXVII, XXVIII, and XXIX.

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THE changes which take place during and subsequent to Stage G are mainly changes of growth and histological differentiation. The most important organs which have not yet made their appearance by the close of Stage F, are the crural glands and tracheæ. The origin of the latter is, I regret to say, still hidden from me. The remaining organs have acquired, in all essential respects, the adult relations by the close of Stage F.

#### THE ECTODERM.

In Stage G, the ectoderm retains the characters already described in Part III, p. 472. It forms an extremely thin, much vacuolated layer over the greater part of the body, and the nuclei are far apart and in a single layer (fig. 5). In embryos of this age, the ectoderm does not contract when the embryo is preserved, and no doubt its extreme tenuity is due to this fact. On the ventral organs the ectoderm is thicker and the nuclei in more than one layer and close together. On the dorsal hump also, the ectoderm still remains thick, with a large amount of protoplasm external to the nuclei.

The dorsal hump, however, has already begun to atrophy ; it eventually completely vanishes.

The general ectoderm possesses a large number of vacuoles, and in certain places the nuclei are aggregated together in masses, and are smaller than elsewhere, forming the rudiments of the future spiniferous sense-organs. The latter give rise to the white spots seen on the skin of embryos of this age.

In *P. Balfouri*, and, to a slight extent, in *P. capensis*, the dorsal ectoderm contains a number of highly refractile globules (Pl. XXVI, figs. 1—4). These are probably yolk globules. They seem to be most numerous in the dorsal hump. The whole dorsal ectoderm of *P. Balfouri* is thicker than the ventral, and partakes, to a certain extent, of the character of the ectoderm of the dorsal hump.

In the later stages, in embryos just before birth, the dorsal ectoderm is highly protoplasmic and much striated, and contains very few, if any, vacuoles (Pl. XXVIII, fig. 12), while the ventral ectoderm is much vacuolated, and retains the characters it possessed at Stage *g*. That is to say, the nuclei lie in the outer part of the layer, the inner parts being reduced to fine unstained strands passing between the vacuoles.

The further changes in the general ectoderm need no special description. The nuclei come closer together, the vacuoles disappear, a cuticle is formed on the outer surface, and the adult condition gradually acquired. The claws of the jaws and legs, and the spines of the sense-organs, are special developments of the cuticle.

The following ectodermal organs require a special description, and will be considered separately and apart from the general ectoderm :

1. The ventral organs.
2. The nervous system.
3. The slime-glands and crural glands.

On the origin of the TRACHEÆ I have no observations. They seem to arise very late, and have hitherto escaped my observation.

## THE VENTRAL ORGANS.

For the origin and general history of these organ I must refer back to Part III, p. 476, and to Kennel (No. 1). They consist of segmented thickenings of the ectoderm, placed between the appendages and composed of two halves, which are in contact in the middle ventral line (Pl. XXVI, fig. 5). During Stage  $\alpha$  they possess two kinds of nuclei: the surface layer of oval, and an inner mass of more rounded elements. The latter are much inclined to drop out in the sections, leaving a surface layer of nuclei and thin protoplasmic strands passing inwards.

From what has been said as to their history it is obvious that the ventral organs represent a portion of the ectoderm, from which the central nervous system was constricted off. They correspond in number with the segments, and are therefore twenty in number in *Capensis*.

1. The ventral organ of the first somite is probably, as Kennel has suggested, represented by the cerebral grooves. These become completely cut off from the surface ectoderm and form the hollow appendages attached to the ventral side of the brain of the adult (Pl. XXVI, figs. 2, 3, and No. 2, fig. 19, c, d). The walls of these vesicles appear to consist of nervous tissue.

2. The ventral organs of the jaws (Pl. XXVI, fig. 4, v. o. 1) come to lie in the buccal cavity on each side of the mouth at the base of the jaws. They differ from all the posterior ventral organs in not coming into contact with one another in the middle ventral line. They remain in the ectoderm, and appear to retain a connection with the posterior lobe of the brain, or anterior part of the circumpharyngeal commissure.

3. The ventral organs of the oral papillæ join one another ventrally and become divided into two parts by the lips—an anterior contained in the posterior region of the buccal cavity, into which the salivary glands open; and a posterior part on the ventral side of the body just behind the mouth. The intrabuccal part remains in connection with the



lateral nerve-cords (No. 2, fig. 14), and these two connections, together with the interposed ventral organ, contribute what Balfour has called the second commissure between the ventral cords.

The posterior part of this ventral organ behaves exactly as do those about to be described.

4. The two halves, of which each ventral organ of the seventeen ambulatory legs at first consist, join one another ventrally, remain as part of the ectoderm, and appear to retain a cellular connection with the lateral nerve-cords (Pl. XXVI, fig. 5). I could not be certain of this connection in the case of every ventral organ; but Kennel asserts that it exists, and I am inclined to agree with him.

#### NERVOUS SYSTEM.

The early development of the central nervous system is described in Part III, pp. 473—475 and 481. In Stage *r* the cerebral grooves are still open (Part III, fig. 33), and the ventral cords are in close contact and still continuous with the thickened ventral ectoderm. The white matter has also made its appearance along the whole length of the dorsal side of both brain and spinal cord.

In Stage *g* two important changes have taken place. (1) The cerebral grooves have become converted into closed vesicles (Pl. XXVI, figs. 2 and 3) and entirely cut off from the superficial ectoderm. (2) The ventral cords have withdrawn themselves from the ventral ectoderm, though they still appear to be attached to the latter by marked cellular processes (fig. 5, Pl. XXVI).

**The Brain.**—The structure of the brain in Stage *g* is shown by the series of sections figured (figs. 1—4, Pl. XXVI). Excepting the increase in the amount of white matter and the closure of the cerebral grooves it is essentially the same as in Stage *r*. In front the two lobes of the brain, though in close contact, are separate from one another (Pl. XXVI, fig. 1). They are continued forwards into the antennæ as the antennary nerves (vide Part III, p. 480). The white matter is

dorsal and extends somewhat into the centre of the lobes. It may be described (vide Balfour, No. 2) as consisting of three horns: viz. a dorso-lateral (*a*), a ventro-lateral (*b*), and a dorsal (*c*). It is continued forwards along the dorsal sides of the tentacular nerves.

At a little distance behind the eyes the central lobe of white matter and the cells dorsal to it become continuous with the same structures on the opposite side (Pl. XXVI, fig. 2). A little farther back the connection between the two brain lobes is effected only by the white matter, the dorso-median patch of cells entirely disappearing (Pl. XXVI, fig. 3). A few sections farther back the latter again appear, and their appearance is soon followed, in the section series, by the separation of the cerebral lobes (Pl. XXVI, fig. 4).

The ventral appendages of the brain have already been dealt with (p. 375).

**The Eyes.**—At the close of Stage E the eyes are closed vesicles, connected by their ventral corners with the brain immediately external to the white matter (Part III, fig. 22 *a*). The connection, which is at first a broad one, has in Stage G become constricted to a narrow pedicle—the optic nerve—connecting the inner wall of the optic vesicle with the brain (Pl. XXVI, fig. 1); at the same time the nuclei withdraw from the optic nerve and from the portions of the wall of the optic vesicle and of the brain, which connects the optic nerve (fig. 1). In this manner the white matter of the so-called optic ganglion of the adult is established, and the optic nerve comes to consist entirely of white matter. The layer which will form the rods in the adult eye appears at a very early stage as a result of the withdrawal of the nuclei of the thick inner wall of the vesicle from the internal surface (Part III, fig. 22 *a*, and Pl. XXVI, fig. 1, *rods*). The pigment and lens have not yet been formed. The eye, therefore, in Stage G (Pl. XXVI, fig. 1) consists of a vesicle with a thin outer wall closely subjacent to the epidermis, which is very thin over the eye, and of a thick inner wall lying close to and connected with the brain by a cord of nerve-fibres. The inner wall further

presents a patch of white matter at the point of entrance of the optic nerve, and a layer of white matter (the rods) next the lumen of the vesicle. The pigment appears in January at the junction of the layer of rudimentary rods and the nuclei. The lens is formed at about the same time, as a secretion of the wall of the vesicle. It lies within and fills up the cavity of the vesicle. This condition of the eye is practically that of the adult.

#### THE VENTRAL CORDS.

The early history of the ventral cords is given on p. 475 of Part III. In Stage F they are still in close contact with the ectoderm, but an indistinct line of separation can generally be seen between them (Part III, fig. 39). In Stage G the separation is complete and distinct, though they still remain connected at intervals by cords of cells with the ventral organs (Pl. XXVI, fig. 5). It is in Stage G also that the **commissures** between the ventral cords and the main **nerves** first become apparent. The commissures between the two nerve-cords are very numerous. They extend in this stage from the ventro-median corner of the cords towards the ectoderm, where they lie in close connection with some rather loose fibrous tissue, which is found at this stage everywhere beneath the ectoderm. They consist of fibrous matter, and can be easily traced into the white matter of the cords.

The efferent nerves arise from the outer border of the cords, directly from the white matter. They are very numerous (Balfour, No. 2), but there are, opposite each leg, two—the pedal nerves—which are much larger than the others and more easily observed. These two arise, the one immediately in front of the nephridium, and the other behind it. In Stage G, when they are first apparent, they consist of close bundles of fibres passing out from the white matter (Pl. XXVI, fig. 5, *nerve*) and continuous with a loose plexus of fibres placed immediately within the ectoderm of the ventral side of the legs (*neuro-musc.*). It therefore appears that the commissure between the nerve-cords, the efferent nerves, and the fibrous

matter beneath the ectoderm, all become distinctly apparent at about the same time in Stage  $\alpha$ ; but how and when they are developed I am unable to say. As may be seen from an inspection of the sections (Part III, figs. 37—39) there is in Stage  $\alpha$  a certain amount of this fibrous tissue, especially at the ventro-lateral corners of the body, close to the outer border of the nerve-cord, and in the nerve-cords themselves as the white matter, and I have no doubt that it is present at a still earlier stage, though masked by the large amount of nuclei present. In fact, it may be said of this tissue generally, that it does not become a marked feature of the sections until the organs separate from one another and leave room for the previously closely-packed nuclei to spread out, and, as in the case of the white matter of the nerve-cord, partly to withdraw themselves from it (cf. Pl. XXVI, fig. 5, and Part III, fig. 39). In whatever manner this tissue may be developed, I think there can be little doubt that it is from its first appearance a continuous tissue, that is to say, the circular fibres at *circ. musc.* in Pl. XXVI, fig. 5, are continuous with the network at *neuro-musc.*, which, in its turn, is continuous with the bundle of fibres forming the nerve, and so with the fibrous matter of the nerve-cords. It thus appears, so far as I have been able to observe the development, that the nerves are not formed as outgrowths from the central nervous system, but are parts of a network which originally existed when the nerve-cords were part of the surface ectoderm. In Stage  $\alpha$ , the network is clearly continuous with the surface ectoderm (Pl. XXVI, fig. 5). With regard to the commissures connecting the ventral nerve-cords, it seems to me that they also are differentiated *in situ* from the median ventral ectoderm at a time when the nerve-cords were still parts of the surface ectoderm. I have already said that I do not know the manner in which this network develops; part of it is undoubtedly formed around the ectodermal nuclei, e. g. the white matter of the cords, the commissures between the cords; some of it, on the other hand, has, from the first, a relation to the mesodermal nuclei, e. g. the circular fibres at *circ. musc.*, and the network on the ventral side of the feet at



Pl. XXVI, fig. 5, *neuro-musc.* The nerves, therefore, are to be regarded as special differentiations of a pre-existing network, the origin of which is not known, but which at first pervades and is continuous throughout the whole ectodermal and mesodermal tissues of the body.

#### SLIME-GLANDS AND CRURAL GLANDS.

The **slime-glands** are entirely ectodermal products. Their early development has been described in Part III, p. 482, and the later changes being simply processes of growth, I have nothing to add to the account there given.

The **crural-glands** appear very late. In embryos of April almost ready to be hatched they have the form of shallow invaginations of ectoderm immediately external to the opening of the nephridium (Pl. XXVII, fig. 11). They seem to be entirely derived from the ectoderm, but I have no details as to their development. I could find no trace of the enlarged crural gland of the last leg of the male in the oldest embryos which I have examined.

**The Stomodæum and Proctodæum**—The early history of the sestructures has already been given in Part III, pp. 482, 485, 486.

The mesodermal investment of the anterior part of the stomodæum becomes very thick, while that of the posterior part remains comparatively thin. The lining cells secrete a cuticular layer. The anterior part becomes the pharynx, and the posterior the œsophagus of the adult.

The proctodæum also acquires a cuticular lining and a well-marked mesodermal investment. It becomes the rectum of the adult.

#### THE ENDODERM.

In Stage G the endoderm is reduced to a layer of extreme tenuity (Pl. XXVI, fig. 5). It soon, however, begins to increase in thickness, and in embryos almost ready for birth has the form represented in Pl. XXVII, fig. 11. The nuclei are placed in the deeper parts of the layer, and the protoplasm

stains deeply and contains a large number of granules. The endodermal part of the alimentary canal is without glandular appendages of any kind. In old embryos the enteron generally contains a deeply-staining material with a number of highly refractile particles in suspension. This substance is probably a secretion of the endoderm cells. The contents of the alimentary canals of the free-living adults is permeated by a number of similar highly refracting bodies.

#### THE MESODERM.

The later history of the mesoderm, i. e. the tissues derived from the walls of the somites, will best be considered under the following four heads, viz :

1. The muscles.
2. The vascular system.
3. The nephridia.
4. The generative organs.

Whether any part of the cutaneous mesodermal structures are ectodermal in origin is, as I have already hinted in dealing with the nervous system, impossible to decide, because of the intimate connection which is established between the ectoderm and the somatic walls of the somites, at almost the first appearance of the latter (vide pp. 487, 488, Part III), and which remains during the whole development (see above (p. 379).

#### THE MUSCLES.

The cutaneous muscles arise from the subectodermal fibrous network which has been already mentioned, and which in Stage F was crowded with the nuclei of the ventro-lateral corners of the somites. The fibres of the outer part of this network arrange themselves in a circular manner, and form the circular muscles of the body wall. At first the fibres are extremely scanty (Pl. XXVI, fig. 5, *circ. musc.*), but they soon become more numerous. Nuclei are found at intervals amongst them (Pl. XXVIII, fig. 13). The longitudinal muscles appear somewhat later within the circular muscle in seven patches, viz. two

dorsal (Pl. XXVIII, fig. 13), two lateral, two ventro-lateral, and one medio-ventral between the nerve-cords. These patches gradually enlarge into the corresponding muscular bands of the adult. They contain nuclei which have often a peculiar, irregular shape (Pl. XXVIII, fig. 13). The muscles, both longitudinal and circular, are deposited outside the commissures connecting the ventral nerve-cords.

The muscles of the feet seem to be derived from the fibrous plexus shown in Pl. XXVI, fig. 1, and are shown at a later stage in Pl. XXVII, fig. 11). The origin of the transverse septa dividing the body cavity into a central and two lateral compartments has already been described (Part III, pp. 493 and 495, figs. 9, 21*a*, 24, 39, &c., *v. s.*). They arise as outgrowths of the ventral corners of the somites.

The contractile tissue of the gut wall and internal organs generally, is derived from the wandering cells, which themselves appear to be derived from the walls of the mesodermal somites.

#### THE BODY CAVITY AND VASCULAR SYSTEM.

As was first pointed out by Lankester, the Arthropoda are distinguished from all other animals by the possession of paired ostia, perforating the wall of the heart and putting its cavity in communication with the pericardium. The pericardial cavity of Arthropoda, therefore, contains blood, and in this respect differs fundamentally from the similarly named cavity in other animals. Not only does the pericardial division of the body cavity contain blood, but the general body cavity, and in *Peripatus* all the compartments of the latter are also vascular tracts; and it is important to distinguish by a special name this vascular type of body cavity from the non-vascular or *CÆLOMIC* type which is found well developed in *Annelida* and *Vertebrata*. The term "*HÆMOCÆLE*," which has been suggested by Lankester for this purpose, seems a convenient one, and I propose to adopt it.

The development of the *hæmocœle* of *Peripatus* has been already fully described in Part III, p. 499, et seq., and p. 510;

and I have but little to add to the account there given. It is derived in part from a system of species developed within the mesoderm, and in part from spaces arising between the ectoderm and endoderm. The diagrams (Pl. XXIX, figs. 14—17) will enable the reader to understand at a glance the origin of the various parts of the vascular tracts and their relation to the coelom.

In Stage g the **heart** becomes a tube with thin walls and flattened nuclei, lying freely in the pericardial cavity, with cords of cell projecting from its walls into the latter. These cords, the origin of which I have not been able to make out—they first appear in Stage f (Part III, figs. 43, 45, 46, *c. c.*) when the dorsal divisions of the anterior somites are disappearing—seem to become transformed in the later stages into a very remarkable tissue. The structure of this tissue, which may be called the **pericardial network**, or reticular tissue of the pericardium, will be best seen by reference to Pl. XXVIII, fig. 13, which represents a transverse section through the dorsal part of an embryo shortly before birth.<sup>1</sup> The wall of the heart is prolonged into delicate processes, which are continuous with a network occupying a considerable part of the lateral region of the pericardium. This network contains round nuclei in its nodes, and is continuous with the floor and roof of the pericardium. Sometimes the nuclei occur singly, but often they occur in masses (right hand side of fig. 13), which often have the appearance of multinucleated cells lying freely in the pericardium. A careful examination, however, shows that they are nodes of the network already described, and that they only differ from the other nodes in possessing more than one of the round nuclei. Occasionally an apparently free cell with one nucleus may be seen lying in the spaces of the reticulum. This reticular tissue is, I think, derived mainly from the strings (*c. c.*) of the earlier stages, and it persists as the pecu-

<sup>1</sup> The apparent fusion of the dorsal and ventral walls of the heart to the dorsal and ventral walls of the pericardium in this figure is due to the contraction of the specimen. The heart at this stage, excepting for the network about to be mentioned, lies quite freely in the pericardium.



liar cellular tissue which has been described by Gaffron (No. 3) in the pericardial cavity of the adult. Gaffron compares this tissue to the fat bodies of other Tracheates, a comparison with which I am inclined to agree, although I am not aware that fat bodies are as a rule present in the pericardium.

Mr. Heathcote, however, informs me that in the Myriapoda a portion of the fat body does lie in the pericardium, and resembles in its relation to the heart the pericardial tissue of *Peripatus*. A tissue exactly like the pericardial tissue is found in the lateral compartment of the body cavity (Pl. XXVII, fig. 11). It has been noticed by Balfour and Gaffron. It seems to me probable that this tissue, which lies in the vascular system, is of the same nature as the lymphatic tissue of the Vertebrata, with which it undoubtedly presents many points of resemblance. The botryoidal tissue of Leeches (Lankester) and the brown cells of Chætopoda may possibly fall into the same category. The former presents very much the same relations to the vascular system, but the latter differs by lying in the cœlom.

In Stage g the horizontal septum which divided the cerebral compartment of the body cavity into a dorsal (*b. b. c.*) and ventral (*b. b. c.*, Part III, fig. 43) chamber breaks down.

Both the pericardial and lateral compartments of the body cavity (hæmocœle) seem to communicate with spaces amongst the muscles of the body wall. One such set of spaces is especially conspicuous between the ectoderm of the ventral body wall and the circular muscles (Pl. XXVII, figs. 11, 17). This system of spaces, which is probably segmentally arranged, communicates with the spaces in the legs. It is, I think, the blood in these ventral vascular channels which exudes through the ventral organs when the animals are contracted by the action of chloroform.

The **ostia** of the heart appear to arise in Stage g. I have no satisfactory observations of them. They are, I think, confined to the posterior end of the heart in the Cape species.

The main vascular tracts, therefore, are five in number, or, to put it in another way, the HÆMOCŒLE is divided into five

main chambers: (1) the central compartment of the body cavity; (2) the heart; (3) the pericardial cavity; (4) the two lateral compartments or lateral sinuses (in which the nerve-cord and salivary glands lie). In addition to these there are the leg cavities, which contain the nephridia and communicate with (4). Of these the central compartment, lateral sinuses, and heart are free for the most part from traversing tissue, while the pericardial chamber and the leg cavities are broken up by reticular tissue, and the leg cavities by muscles as well.

### THE NEPHRIDIA.

An account of the nephridia up to Stage *f* will be found in Part III. By Stage *g* they have practically attained the adult condition, and to complete my account of their history it will only be necessary to describe their final condition, for which purpose I have chosen a stage shortly before birth. I propose at the same time to give a short recapitulatory account of their whole history, under the head of the somites from which they are respectively derived. The general changes which the somites undergo will be rendered clear by a glance at the diagrams on Pl. XXIX, figs. 14—17. It must be remembered that I am only dealing here with the cavity contained in the somites, i. e. the *CÆLOM*, and its immediate lining. The walls of the somites, particularly the somatic walls, become greatly thickened and hollowed out. The tissues and cavities so formed give rise to muscles, connective tissue, and parts of the vascular system, as has already been fully described.

**SOMITES OF THE ANTENNÆ** (Part III, p. 504).—The first somites send down a diverticulum outside the brain towards the skin (Part III, figs. 19 *b*, 50, *s. so.* 1) and then divide into two parts (Part III, fig. 51, *s.* 1). They seem to have completely disappeared by Stage *g*. The ventral diverticulum of Stage *e* is obviously the rudiment of a nephridium.

**SOMITES OF THE JAWS** (Part III, p. 506).—The second somites do not give rise to even a rudiment of a nephridium. They seem to disappear.

SOMITES OF THE ORAL PAPILLÆ (Part III, p. 507).—The third somites send out a ventral diverticulum (Part III, fig. 21 *c.*), which acquires an opening to the exterior (Part III, fig. 23 *e.*). They become divided into a dorsal and ventral part (diagram, Pl. XXIX, fig. 14), of which the dorsal vanishes, while the ventral persists in connection with the opening above mentioned, and is at first placed in the appendage (Part III, fig. 23 *e.*). This ventral or appendicular part is the nephridium of the somite, and becomes the **salivary gland** of the adult. The general form of this nephridium at the close of Stage *r* is well shown by the diagram (Pl. XXVII, fig. 6). It consists of a tubular part (*l. s. t.* 3, *sal. gl.*), opening in front on the ventral surface of the body (*o. s.* 3) within the lip and ending blindly behind, and of a vesicle (*l. s. v.* 3) opening into the tubular part a little in front of its termination. The structure and relations of these parts to each other are illustrated by the three transverse sections figured in Part III, figs. 37, 38, and 39, and taken along the lines marked 37, 38, 39 in the diagram (Pl. XXVII, fig. 6). The subsequent changes which this organ undergoes are unimportant. They are illustrated by the diagram Pl. XXVII, fig. 7, and by figs. 8 and 9, taken from transverse sections of an embryo shortly before birth, along the lines 8 and 9 in fig. 7.

The tubular part has become much elongated (Pl. XXVII, fig. 7, *sal. gl.*), so that it now extends a considerable distance behind the point of communication with the internal vesicle. It constitutes the salivary gland of the adult, and lies, as is well known, in the lateral compartment of the body cavity (lateral sinus). The walls of the vesicle (*l. s. v.* 3) have become much thicker. They consist (Pl. XXVII, fig. 8) of a layer of nucleated, richly vacuolated protoplasm. Finally, the portion connecting the tubular part (*l. s. t.* 3) and the vesicle (*l. s. v.* 3) has become elongated into a tube running forwards from the tube to the vesicle, as shown in the diagram (Pl. XXVII, fig. 7). This communicating portion, as shown in Pl. XXVII, fig. 9, is closely applied to the dorsal side of the tubular part.

The internal vesicle, which, together with the communicating tube, has hitherto been overlooked, persists in the adult, and probably constitutes an important functional part of the salivary gland.

SOMITES OF THE FIRST, SECOND, AND THIRD LEGS (Part III, p. 507 et seq.).—The third, fourth, and fifth somites divide early into a dorsal and ventral portion, of which the dorsal vanishes, while the ventral acquires an opening to the exterior and persists as the nephridium. The condition of these nephridia in Stage F is shown by Part III, fig. 40. The subsequent changes are very slight, and may be gathered from an inspection of Pl. XXVII, fig. 10, which is from a transverse section through the third leg of an embryo almost ready for birth. The nephridium (Pl. XXVII, fig. 10) consists of a thin-walled internal vesicle contained in the leg compartment of the body cavity and communicating by a straight tube with the external opening on the ventral surface. The wall of the vesicle consists of a ragged protoplasmic layer, with here and there a round nucleus.

SOMITES OF LEGS 4 TO 12.—The early history of the seventh to the fifteenth somites inclusive is similar to that of the somites of the first three legs; but in the later stages the tubular part of the nephridium becomes elongated, coiled, and divided into at least three regions (Pl. XXIX, fig. 17, diagram). (1) The part next the external opening is dilated into a vesicle—the external vesicle—which is connected with the external opening by a narrow tube (Pl. XXVII, fig. 11). (2) The vesicle opens into a long coiled tube, which forms the greater part of the nephridium. It is cut across twice in the transverse section from which fig. 11 was taken. It is continuous with (3) a short terminal portion in which the nuclei are very closely packed together. This terminal portion opens with everted lips into the thin-walled, internal vesicle, and constitutes the so-called funnel of the nephridium. The external opening of the nephridia of the fourth and fifth legs are at first immediately outside the nerve cord, as in the case of the others. Their adult position is due to a secondary shifting.



SOMITES OF LEGS 13 TO 17 (Part III, p. 510).—The dorsal divisions of these somites persist as the generative organs, and will be described below (Pl. XXIX, diagrams figs. 15—17). The ventral divisions develop as in the legs immediately preceding.

SOMITES OF THE ANAL PAPILLÆ (or in *P. Balfouri* of the eighteenth legs).—I have nothing to add to the description given on p. 513 of Part III. They persist entirely as parts of the generative ducts. For descriptions and figures of the isolated nephridia of the seventeen legs of the adult I must refer the reader to Balfour's memoir (No. 2), pp. 32—35, and Pl. XIX, figs. 27, 28. I have nothing to add to his description, excepting the fact that the terminal portions of the nephridia do not open into the body cavity, which is a vascular space and not cœlomic, but, as shown in Pl. XXVII, fig. 11, and in diagram fig. 17, into a thin-walled vesicle, which is directly derived from the original somite.

I think there can be no doubt that the vesicle of the nephridia of the first three legs is homologous with the internal vesicles of the posterior nephridia and not with the collecting, or external vesicle. A comparison of figs. 10 and 11 on Pl. XXVII, shows that the tubular part of the first three nephridia is very different from the narrow tube leading outward from the external vesicle in the posterior nephridia; though it is without the closely-packed nuclei in the terminal so-called funnel. Further, the structure of the wall of the vesicle itself resembles that of the internal vesicle of the posterior nephridia and not that of the collecting vesicles.

The external cuticle is only prolonged for a very short distance into the neck of the collecting vesicle.

#### THE GENERATIVE ORGANS.

The early history of these organs has already been fully described in Part III, pp. 511—515, and I have but little to add to that description. They first appear in the endoderm as large round nuclei (Part III, figs. 26, 27), which migrate into the splanchnic mesoderm (Part III, fig. 41) of the dorsal divisions of

the sixteenth to the twentieth somites, where they acquire a protoplasmic investment (Part III, figs. 43, 47). The parts of the somites containing them persist as the generative tubes, and become continuous behind with the twenty-first somite (Part III, figs. 42, 44), which does not divide into a dorsal and ventral part but acquires a ventral opening in the same position as the preceding somites. The opening soon, however, shifts to the middle line, where it joins its fellow, so as to form the single generative opening of the adult. In all probability the greater part, if not all of the ducts of the adult, are derived from the twenty-first somite; the dorsal divisions of the five preceding somites forming the generative glands only.<sup>1</sup>

In Stage G the generative organs form two tubes lying in the central compartment of the body cavity and closely applied to one another in the middle line (Part III, figs. 47, 48).

I cannot say when the generative cells begin to show sexual differences. The appearance of the sections referred to (Part III, figs. 47, 48) would lead one to suppose that the specimen was a female, and I have but little doubt that it was. At the same time, I must mention that I have never seen anything at this stage which I could call a male.

In January sexual differences are undoubtedly manifested by the generative tubes. Those of the females presented very much the appearance of the earlier stage. In the male the nuclei were smaller and more numerous, and the lumen was narrower. In fact, the organs differed very much in the same way that they do in ripe embryos. Pl. XXVII, fig. 12, is from a transverse section of a female embryo almost ready for birth, and fig. 13 from a male embryo of the same age. At this

<sup>1</sup> This view would be confirmed in the case of the female if it could be proved that my suggestion (Part III, p. 514) that the receptaculum ovarum of the neotropical species is part of the somite which gives rise to the generative opening and outer part of the generative ducts, and homologous with the internal vesicle of the nephridia. The case of the male is more difficult, but probably the testes (prostates of Moseley and Balfour) only, *i. e.* the parts in front of the swollen vesiculæ seminales (testes of Moseley and Balfour), are alone derived from the dorsal divisions of the generative somites.

stage the ovarian tubes communicate with one another at their extreme front ends, and behind where they pass into the oviducts. In the male the tubes are considerably twisted; I could not make out any distinct trace of the vesicula seminalis.

I regret to say that I have not paid much attention to the histological development of the sexual glands. The first trace of the sexual organs is the round nuclei of the endoderm. When and how these acquire a cell body I cannot say. They certainly have the latter by Stage G (Part III, figs. 47, 48). The follicular nuclei are the nuclei of the splanchnic mesoderm, which closely apply themselves to the germinal nuclei as soon as the latter emerge from the endoderm. The follicular nuclei appear, therefore, before the protoplasm of the sexual cells (Part III, fig. 26). In Stage G areas of protoplasm, indistinctly marked off from one another, could be distinguished round the larger nuclei (Part III, figs. 47, 48). In the females of the stage just before birth the boundaries of these areas were slightly more marked, but still indistinct (Pl. XXVII, fig. 12). In the male of this stage there are no lines separating the protoplasm round the granular nuclei of the testes into areas (Pl. XXVIII, fig. 13).

The general bearing of the facts of development of the cœlom and body cavity of *Peripatus* is fully dwelt upon in Part III of this series. I have but little doubt that the same method of development will be found in other Arthropoda. If I am right in this view it must be admitted that the Arthropoda are cœlomite animals, that their generative cells are products of the cœlomic epithelium, and that the generative ducts are modified nephridia.

The cœlom of *Peripatus* does not extend into a perivisceral or body cavity, but remains small, discharging only the functions of excretion and reproduction. The functions of a perivisceral cavity are discharged by the vascular system, in which indeed the cœlom is contained (Pl. XXVII, figs. 10, 11, 13, and diagram, fig. 17) in exactly the same way as the intestine of a mammal is contained in the cœlomic body cavity. The

condition of the cœlom and vascular tracts in the adult and the relation of the cœlom to the vascular body cavity is clearly illustrated by the diagram (Pl. XXIX, fig. 17). It is commonly said that in the Arthropoda the generative ducts are continuous with the glands, and in this they are contrasted with the Annelida and Vertebrata. As a matter of fact, however, the generative ducts, in *Peripatus* at least, present exactly the same relation to the generative glands as do the oviducts of a dogfish or earthworm to the ovaries of these animals; that is to say, like the latter, the generative ducts open into the cœlom, and the ova are products of the cœlomic epithelium.

It is important to notice that in *Peripatus* the nephridia are parts of the cœlom (Pl. XXIX, diagram, fig. 17), just as they are in Elasmobranchs. They are commonly spoken of in a manner which implies that they have but little to do with the cœlom beyond opening into it. This way of speaking of them is calculated to mislead. The nephridia are direct differentiations of part of the cœlom (diagrams, figs. 13—17, and figures in Part III illustrating their development).

A negative feature, which has often been put forward as characteristic of the Arthropoda, is the apparent absence of nephridia. The nephridia of *Peripatus* have generally been considered as a primitive and peculiar feature. Lankester,<sup>1</sup> however, some time ago (No. 54, p. 516), suggested that the coxal glands of *Limulus* and the antennary glands of Crustacea were nephridia, and that the peculiar "end-sacs" described by Gulland in the coxal glands of the young *Limulus*, and the internal vesicle of the Crustacean anten-

<sup>1</sup> Lankester's words were: "The observations here recorded on the structure and connections of the immature coxal gland of *Limulus* tend to render it probable that the green glands of Crustacea are also to be regarded as a pair of modified nephridia;" and he goes on to say that "it seems not improbable that the so-called end-sac of these glands is not part of the nephridium, but is developed from the connective-tissue space (cœlomic space) into which the true tubular nephridium opens." The distinction implied by these last-quoted words between the nephridium and cœlom is not justified by embryology, as I have just pointed out.



nary gland described by Grobben (No. 55), were part of a true cœlomic space. The discovery of the end-sacs in *Peripatus*, and of their method of development, entirely confirms Lankester's view. And it is interesting to notice that the end-sac of the Crustacean green gland, as figured by Grobben, resembles somewhat in the structure of its wall the end-sacs of the *Peripatus* nephridia.

In the Leeches the nephridia are stated by Bourne (No. 4) and other observers to communicate with the vascular system. I think, however, it is worth while to bear in mind the possibility of there having been a mistake on this point. It is possible that the nephridia in the Leeches may, as in *Peripatus*, end in a closed vesicle which lies in, but does not open, into the vascular system. Such vesicles might quite well have been overlooked by the able observers who have dealt with the subject, as they undoubtedly were overlooked in *Peripatus*.

It is interesting to notice the resemblance which would exist between the transverse section of *Peripatus* (Pl. XXIX, fig. 17) and the transverse section of a Leech, if the blood tracts of the former were more broken up, and the nephridia of the latter did not open internally into the vascular system.

#### LIST OF PAPERS REFERRED TO.

1. KENNEL, J.—“Entwicklungsgeschichte v. *Peripatus Edwardsii* u. *torquatus*,” Theil ii, ‘Semper’s Arbeiten,’ Bd. vii.
  2. BALFOUR, F. M.—“Anatomy and Development of *Peripatus Capensis*,” ‘Quart. Journ. Micr. Sci.,’ vol. xxiii.
  3. GAFFRON, E.—“Beiträge zur Anatomie u. Histologie v. *Peripatus*,” ‘Schneider’s Zoologische Beiträge,’ Bd. i.
  4. BOURNE, A. G.—“Contribution to the Anatomy of the Hirudinea,” ‘Quart. Journ. Micr. Sci.,’ vol. xxiv.
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EXPLANATION OF PLATES XXVI, XXVII, XXVIII,  
and XXIX,

Illustrating Mr. Adam Sedgwick's paper on "The Development of the Cape Species of Peripatus. The Changes from Stage G to Birth."

*List of Reference Letters.*

*a.* Dorso-lateral horn of white matter of brain. *b.* Ventro-lateral horn of white matter of brain. *b. app.* Body cavity of appendage, a blood-space. *b. lat.* Lateral compartment of body cavity (space formed in parietal mesoderm); a blood-space. *cer. ves.* Cerebral vesicles or ventral appendages of brain. *circ. musc.* Circular muscles of body wall. *crur. gl.* Rudiment of crural gland. *E.* Central lobe of white matter of brain. *l. s. t.* 3. Tubular part of nephridium of third somite. *l. s. v.* 3. Internal vesicle of nephridium of third somite. *neuro-musc.* Network of fibres, so-called because it gives rise to nerves and muscles; it is continuous with the lateral pedal nerve, and is apparently composed of a substance like the latter and the white matter of the cord. It is derived from a compact mass of nuclei present in the previous stages at the same point. *or. pap.* Oral papilla. *o. s.* 3. External opening of nephridium of the third somite. *sal. gl.* Salivary gland, *sl. gl.* Slime-gland. *v. o.* Ventral organ. *v. o. 1.* Ventral organ of jaws. *v. s.* Septum separating the central from the lateral compartments of the body cavity, called in earlier stages the ventral sheet of somatic mesoderm.

FIGS. 1—4.—A series of transverse sections through the head of an embryo of *Peripatus Balfourii* of Stage G (removed from the uterus on 12th December). One side only of each section is completely drawn. The dorsal ectoderm possesses a large number of highly refractile spheres, probably yolk-spheres, and has contracted on to the brain so as to render indistinct the mesoderm structures between. *a.* Dorso-lateral. *b.* Ventro-lateral. *e.* Central lobe of white matter.

Fig. 1. Through the region of the eye and anterior lobes of the brain. One side only is figured, and the nuclei of the ventral part of the brain are omitted. The section goes through the optic nerve and centre of the optic vesicle. Zeiss's camera, obj. D, oc. 2.

Fig. 2. A little farther back, through the anterior part of the cerebral vesicle (*cer. ves.*) and the region of junction of the two halves of the brain. The dorsal mass of nuclei and the central lobe of white matter have united with the corresponding structures of the opposite side. Ventrally the two halves of the brain are separate.

Fig. 3. A little farther back, through the centre of the cerebral vesicles, and still through the joined part. The dorsal mass of nuclei are absent, and the white matter is broadly exposed dorsally.

Fig. 4. Through the posterior lobes of the brain and the region of the buccal cavity. The ventral organ of the jaw (*v. o.* 1) and the jaw are shown. The oral papilla (*or. pap.*) and slime-gland (*sl. gl.*) are also visible.

Figs. 2—4 drawn with Zeiss's camera, obj. C, oc. 2.

FIG. 5.—Portion of transverse section through the middle region of the body of an embryo of *Peripatus capensis* of Stage G (removed from uterus 16th December). The section passes through the anterior part of a pair of legs. The details are filled in on the left-hand side of the drawing. The section passes through a ventral organ (*v. o.*), with which the nerve-cords are connected by a cellular process, a persistent trace of the original complete continuity between these two structures. The anterior of the two large pedal nerves is shown (*nerve*), leaving the cord as it immediately passes forwards out of the plane of the section; the continuity between it and the neuro-muscular network (*neuro-musc.*), which will eventually develop into the nerves and muscles of the foot, and between it and the circularly disposed network from which the circular muscles (*circ. musc.*) of the body wall will develop, could not be shown in this figure. The walls of the alimentary canal are very thin. *b. lat.* marks the lateral compartment of the vascular body cavity (space formed in parietal mesoderm of early stages). *b. app.* The vascular body cavity of the appendage. Drawn on the table, Zeiss's new camera C, oc. 2.

FIG. 6.—A diagram of the ventral portion of the third somite at Stage F. The vertical lines indicate the planes of the sections Figs. 37, 38, 39 of Part III.

FIG. 7.—Diagram of the ventral portion (nephridium) of third somite at birth. The hinder part of the tube of the preceding stage has elongated backwards to form the long tubular salivary gland (*sal. gl.*).

FIGS. 8—13 are all from embryos just before birth (removed from uterus 19th April). They were all drawn on the table with a Zeiss's new camera, obj. C, oc. 2.

Figs. 8 and 9. Transverse sections through the same structure, along the lines marked 8 and 9 in the preceding diagram (Fig. 7). The vesicle (*l. s. v. 3*) has thick, much vacuolated walls, and is placed dorsal to the tubular part (*l. s. t. 3*). In Fig. 9, the small portion connecting the vesicle and tube is shown closely applied to the dorsal wall of the salivary gland.

Fig. 10. Portion of a transverse section through the region of the third leg of *P. capensis* just before birth. The section passes through the opening of the nephridium, and what I take to be the rudiment of

the crural gland (*crur. gl.*). The whole nephridium is shown in the section. In the actual section the internal vesicle was somewhat more collapsed than in the figure. The funnel and internal vesicle I take to be homologous with the similarly named structures of the posterior nephridia.

Fig. 11. Portion of a transverse section through the region of one of the posterior legs of *P. capensis* just before birth. The section passes through the opening of the nephridium and the rudimentary crural gland. The tubular part of the nephridium is cut in two places, and its terminal portion with the closely-packed nuclei is shown opening into the internal vesicle. The cavity of the leg is traversed by a considerable amount of muscular tissue external to the nephridium, and contains some of the reticular tissue in its dorsal part. The septum separating the lateral sinus from the leg cavity is absent in this region.

Fig. 12. Section through the ovaries of an embryo of *P. capensis* just before birth. On the right side there is an attachment to the pericardium. The dark elongated nuclei are follicular nuclei.

Fig. 13. Dorsal part of a transverse section of a male of *P. capensis* just before birth. In most embryos of this age the wall of the heart is separate (always connected by filaments) from the dorsal body wall and the pericardial floor. The apparent fusion in this section was probably due to contraction of the body. The two patches of dorsal longitudinal muscles are shown.

FIGS. 14—17 are a series of diagrams to show the relations of the coelom and body cavity at successive stages. The lining of the coelom is shaded dark, the light shading indicates the general mesoderm.

Fig. 14. Earliest stage: coelom as a series of separate spaces. The ectoderm and endoderm still in contact: no trace of the vascular space or hæmocœle.

Fig. 14*a*. The endoderm has already separated from the dorsal and ventral ectoderm. On the right-hand side the somite has not yet divided into a dorsal and ventral portion. The first rudiment of the lateral sinus is present in the thickened mesoderm. On the left side the coelom has divided into a dorsal part, which in the anterior part of the body vanishes, but in the posterior part becomes the generative organ; and into a ventral part which becomes a nephridium. The lateral sinus has increased in size, and a space has appeared in the mesoderm of the leg.

Fig. 15. The dorsal division of the coelom has passed dorsalwards, and considerably encroached upon the dorsal of the two blood-spaces formed by the separation of the endoderm and ectoderm. This median dorsal blood-space becomes the heart. Two spaces have appeared in the ventral wall of the dorsal division of the somites; the dorsal of these



becomes the pericardium, the ventral the dorsal part of the central compartment of the body cavity. The ventral blood-spaces have increased in size, but are otherwise unchanged.

Fig. 16. The dorsal divisions of the somites have relatively diminished in size, and been overlapped dorsally by the greatly increased pericardium. The dorsal part of the central compartment of the body cavity has increased in size, but is still separated ventrally by a septum. The ventral blood-spaces have increased in size. The ventral division of the *cœlom* is assuming the form of a nephridium.

Fig. 17. Diagram of arrangement at birth. The two halves of the pericardial cavity have coalesced dorsally and ventrally to the median-dorsal blood-space which forms the heart. The dorsal divisions of the *cœlom* have become constricted off from the floor of the pericardium and the dorsal wall of the enteron, and now lie in the central compartment of the body-cavity and constitute the generative tubes (in the anterior part of the body they atrophy in the floor of the pericardium). The horizontal septum separating the dorsal division of the central compartment of the body cavity from the ventral has vanished. The ventral or nephridial division of the *cœlom* has assumed the form of a nephridium. On the left hand the whole course of the nephridium is diagrammatically shown.

On the Occurrence of numerous Nephridia in the same Segment in Certain Earthworms, and on the Relationship between the Excretory System in the Annelida and in the Platyhelminths.

By

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With Plates XXX and XXXI.

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*Acanthodrilus multiporus*, F. E. B.<sup>1</sup>

THE nephridia of this worm differ in their appearance from those of any other species of *Acanthodrilus* at present known. In a dissection of the worm the nephridia can be recognised as a series of glandular tufts closely adherent to the body wall and to the intersegmental septa; each of the eight setæ often appeared to have a nephridial tuft specially related to it: thus by dissection there seemed to be eight separate nephridia in each segment. This, however, is not invariably the case, and in the anterior segments no relation between the setæ and the nephridia could be detected by dissection.

I have also studied these organs by transverse and longitudinal sections.

By these means I have been able to ascertain that there are more than one pair of nephridiopores in each segment of the body.

These observations depend upon the study of very well-

<sup>1</sup> 'Proc. Zool. Soc.,' 1885.

preserved material, for which I am indebted to Professor Parker, of Otago. One of the numerous specimens which he sent me was so preserved that the nuclei, not only of the nephridia but of the tissues generally, were stained dark yellow, and could not be subsequently stained by borax carmine; accordingly the nuclei were extremely conspicuous in such preparations; and as the nuclei of the nephridial tubules differed in size and shape from other nuclei (e.g. those of peritoneal cells and blood-capillaries), the course of the tubules through the body walls could be easily followed. It must not, however, be inferred that such drawings (e.g. fig. 1) in the plate as illustrate the structure of the nephridial tubules are imaginary, except as concerns the nuclei. They are in every case accurate drawings, so far as I could make them; but the conspicuous nuclei drew my attention to the delicate inconspicuous walls of the tubule, which would otherwise almost inevitably have been overlooked.

The nephridia are arranged, as already stated, in tufts of tubules, closely adherent to the body wall (see figs. 2, 3); their structure is much like that of other earthworms; they consist of tubules with an intracellular duct, some (fig. *n'*) larger than others (fig. *n*). The nephridial tufts are supplied with abundant blood-capillaries, upon some of which are those curious dilatations to which Lankester first drew attention in *Lumbricus*. In spite of the most careful search I have hitherto failed to find any trace of the internal openings of the nephridia.

The external orifices, however, are obvious enough. The disposition of these is illustrated in figs. 1, 2, 3. Figs. 1, 2, 3 represent actual sections, or rather are compiled from a number of sections. Fig. 15 is schematic, and represent what I believe to be the general arrangement of the nephridia in certain segments of the body.

Figs. 2, 3 are copied from sections through certain of the post-clitellar segments, fig. 1 the 8th or 9th.

It will be noticed that the external pores are decidedly more numerous in the anterior segments of the body, while in the

posterior segments they tend to be arranged in accordance with the number of the setæ, i. e. eight per somite. This disposition of the nephridiopores is associated with a corresponding regularity of the nephridial tufts, which tend to break up in the posterior segments into eight separate nephridia. There is, however, a connection between them, as shown in figs. 2, 3. A series of tubules (figs. 1 *n* and 5 *n*) run from seta to seta, and unite the nephridial tufts of these setæ; this tubule for the most part runs within the peritoneum.

The appearances presented, in fact, can hardly be explained, except on the assumption of a network of nephridial tubules. In no Annelid, except in *Pontobdella* (Bourne 5) has the nephridial system been recorded to be a network. I can, however, find no evidence that the nephridial network of one side of the body is continuous with that of the other; nor does there appear to be any connection between the nephridia of successive segments.

The tubules leading to the exterior are, in the posterior segments, nearly invariably related to the setæ; occasionally (fig. 2 *a*) a tubule was observed to perforate the body wall between the setæ, but in this case it must be noted that the tubule passes up a septum of connective tissue, which at this point breaks the continuity of the longitudinal muscle layer. It may be that such septa, which occur here and there, represent the last trace of setæ which have now disappeared. Sometimes (fig. 3 *a a'*) I noticed two nephridial tubules belonging to the same seta. I did not succeed in observing with certainty whether or not they opened on to the exterior by distinct orifices. The ductule is usually embedded in the lax connective tissue which surrounds the insertion of the seta (fig. 4); it passes up as far as the circular muscular layer without undergoing any changes in character, that is to say, the duct is intracellular. At this point the tubule often runs for some distance along the junction between the circular and longitudinal muscles before perforating the former, and opening on to the exterior; in other cases (fig. 4 *b*) the tubule at once perforates the circular muscular layer and the epidermis, and opens on to the exterior.



The distal section of the nephridium where it traverses the circular muscles is somewhat wider than the rest, and is lined by a single layer of small, delicate cells; the duct in this region is inter-cellular. Occasionally the distal section of the nephridium is branched (fig. 2 *b*) and opens by several (three) distinct orifices.

In the anterior region of the body the nephridiopores of each segment are more numerous; they could be easily observed by a simple examination of the cuticle, and lie between the setæ in a more or less regular row. There were over one hundred apertures in each of several segments that I examined in this way.

In transverse sections the nephridial tubules were seen to pass through the body wall, not only in the immediate neighbourhood of the seta (fig. 1), but elsewhere. Very constantly the nephridial tubule did not open by a single pore, but branched, at the junction of the circular and longitudinal muscles, and opened on the exterior by a number of distinct orifices (fig. 1 *b*). This branching of the nephridial duct within the substance of the body wall is paralleled in the case of *Capitella*, where Fischer (8) has recorded a similar branching.

Fig. 15 represents a diagram of what I believe to be the arrangement of the nephridia in one of the posterior segments of *A. multiporus*; it may be compared with fig. 14, which is a corresponding diagram of *Perichæta*. I am not able to give a satisfactory diagram of the anterior part of the body in *Acanthodrilus*.

### *Perichæta*, Schmarda.

The peculiar "tufted" condition of the nephridia in this genus was first made known by Perrier, and has since been commented upon by others. This appearance of the nephridia led me to expect that I should find numerous nephridiopores in each segment. I was, however, unable to put this supposition to the test, until I received quite recently a number of

excellently preserved examples from Bermuda, through the kindness of Mr. Shipley, Fellow of Christ's College, Cambridge. These specimens appear to be identical with Perrier's *P. aspergillum*. The nephridiopores could be easily observed, as in the case of *Acanthodrilus multiporus*, upon the cuticle when stripped off and examined in water. I may take this opportunity of saying that there are other structures which might possibly be confounded with the nephridiopores; these are the impressions of sense cells upon the cuticle<sup>1</sup> which in *Perichæta* often lie between the setæ. A careful examination, however, soon serves to discriminate between the two; the circular bulgings of the cuticle, due to the prominent sense organs, although presenting the appearance of pores under a low power, are readily seen under a high power not to be pores at all, while the nephridiopores are clearly holes in the cuticle.

The latter form a more or less irregular row surrounding each segment and lying between the setæ (fig. 12). Often there are four or five between two setæ. In transverse sections each pore is seen to be continuous with a nephridial tubule; the actual orifice is surrounded (fig. 8) by a very few large cells—smaller, however, than the cells of the epidermis; below these are smaller cells; that section of the tubule which lies within the circular muscle layer, has a wide lumen whose walls are made up of excessively delicate flattened cells. At the junction of the circular and longitudinal fibres the duct becomes intracellular (fig. 10). The nephridial tubules are abundantly supplied with blood-vessels (figs. 10, 11) in their passage through the body walls. The nephridial tubules agree with those of *A. multiporus* in the fact that the duct becomes inter-cellular at the junction of the longitudinal and circular muscles (cf. figs. 6 and 10). Fig. 9 represents the actual number of nephridial tubules and their external orifices in a small portion of the body wall; the figure would be equally correct, so far as my observations go, for any part of the body wall. I should state, however, that I have at present only

<sup>1</sup> Vejdovsky (13), pl. xv, fig. 13a.

studied the anterior region of the body comprising the first sixteen or seventeen segments.

I have never observed any branching of the nephridial tubules in the body wall like that which occurs in *Acanthodrilus* (see fig. 1); but I am not prepared to deny that it may occasionally happen.

So far the nephridial system of *Perichæta* is closely similar to that of *Acanthodrilus*, with only some small differences in detail.

An important point of difference is illustrated in fig. 7; in this figure it will be seen that the nephridial network of one segment is continuous through the septum with that of the next. The nephridial system in fact differs from that of any other earthworm, or indeed from that of any other Annelid except *Pontobdella* (Bourne) (5), in that it forms a continuous network uninterrupted by the inter-segmental septa. Furthermore, there appears to be a perfect continuity between the nephridial system of the right and left halves of the body. The nephridial system of one segment communicates with that of the neighbouring segments at numerous points; there is no question here of a pair of longitudinal ducts such as has been described recently in *Lanice conchilega* (Lang (11), Cunningham 6). The resemblance to *Pontobdella* is very striking, the only difference being that the external apertures in each segment are numerous instead of being only a single pair. With regard to internal apertures (funnels) I can say nothing. I have been entirely unable to find any trace of them.

The diagrams (fig. 13) illustrates what I believe to be the arrangement of the nephridial network and the external pores (*o*) in a few segments. I should say that I cannot pretend to accuracy in the course of the tubules within the cœlom. To reconstruct from a series of sections the course of the comparatively simple nephridium of *Lumbricus* is a hard enough task; to map out accurately the extremely complicated coils of the nephridial network of *Perichæta* is for me an absolute impossibility. I can, however, assert most positively

that the external apertures do not each correspond to a nephridium isolated from its fellows; the nephridial tufts form a continuous layer coating the body wall; there must therefore be a network, although it may not be of course so complete a network as I have sketched in the figure just referred to.

Typhæus, F. E. B., and Dichogaster, n. g.

I have observed numerous nephridiopores in a single segment in both these genera; at present I can only record the fact without giving any details, which I hope to be able to do later.

### The Excretory Organs of Annelids and Platyhelminths.

Two views have been held respecting the relationship of the nephridia in Annelids to those of the Platyhelminths. Gegenbaur has held ('Comp. Anat.,' Engl. trans., p. 177) that there can be no direct homology between the nephridia in the two groups, because, in the Hirudinea at least, these organs are preceded by several pairs of embryonic excretory tubes. On the other hand, Lang and others believe that "the excretory system of the Platyhelminths is the starting point of that of all higher animals," that in fact the nephridia of Annelids are strictly comparable to those of the unsegmented worms.

The former view has recently been extended and defended with great ability by Dr. R. S. Bergh, of Copenhagen (4). The latter view is the one which perhaps finds the most general acceptance among comparative anatomists. Bergh uses arguments which tend to prove that the provisional larval excretory organs of *Polygordius*, of *Eupomatus*, and other *Polychæta*, of the *Hirudinea*, of *Echiurus*, of certain *Oligochæta* (lately discovered by Vejdovsky), and of *Mollusca*, are homologous with each other and with the excretory system of the *Platyhelminths*; the permanent nephridia of these various groups are therefore to be regarded as new formations (in the *Annelida*), or possibly to be derived from the genital ducts of



the flat-worms. Great stress is laid upon the structural identity of the Platyhelminth excretory system with the "head kidney" of larval *Polygordius*, *Chætopods*, and *Gephyreans*. In both there is a system of fine branched tubes formed of perforated cells, which unite to form a pair of wider tubes opening on to the exterior; the internal apertures open through a single cell, the so-called "flame cell;" in many of the larval forms the peculiarly modified flame cell is absent, but the aperture is plugged by a single cell. In the *Hirudinea* and *Oligochæta* there is no longer a special anatomical resemblance to the Platyhelminth; but this is due to the rudimentary condition of the larval excretory organ, rudimentary because there is no free swimming larva.

Another argument is drawn from the apparent independence of the larval and permanent excretory organs in *Annelids*; the fact that in many cases there is no connection between the larval nephridia and those of the adult, and the want of any confirmation of Hatching's statements to the contrary, indirectly favour the hypothesis.

Again, it is pointed out that while the larval nephridia of *Polygordius* lie in the head cavity, the persistent nephridia lie in the coelom; and these two cavities are not similar. On the other hand, the Platyhelminths have no true coelom, only a series of minute clefts and spaces in the mesodermic tissue with which the flame cells are connected, and which form a "primary body cavity," comparable to the primary body cavity or head cavity of the *Annelid* larva.

Dr. Bergh's conclusions largely depend upon his own researches into the nephridia of *Hirudinea*; these have been recently criticised by Whitman (15), who meets Bergh's assertion that the larval nephridia have no connection with the permanent nephridia by an equally positive assertion that they have. With regard to the larval excretory organs of the *Oligochæta*, which have been discovered by Vejdovsky (13) in a variety of types, it is to my mind a significant fact that they occur at the anterior end of the body where no permanent nephridia are developed; furthermore, these organs lie in the

cœlom perforating the mesentery which separates the first from the second segment;<sup>1</sup> hence Bergh's objection to the homology between the larval and permanent nephridia, on the score that the former do not lie in the true cœlom, is removed.

It is not yet a universal belief that a cœlom is absent in the Platyhelminths; in any case, as Lang says, "the entire mesoderm of the Platyhelminths may very well be the equivalent of the entire mesoderm in the Enterocœla," apart altogether from the question of the enclosed cavity. In Capitellidæ the nephridia seem, from Eisig's description, to lie in the somatopleure, i. e. not in the cœlomic cavity at all. The greater portion of the nephridium in *Polygordius* is similarly situated; and Fraipont in his work upon the Archiannelida (9) remarks upon this as an archaic character. Again, Weldon (14) has brought forward reasons for believing that in *Dinophilus*, "which is literally no more than a larval Annelid with reproductive organs" (Lang), the body cavity may be really strictly comparable with that of Annelids, seeing that in *Saccocirrus*—an undoubted Annelid—the body cavity may be secondarily (?) invaded by a ramifying network of mesodermic cells.

In *Dinophilus* there are excretory organs of the Platyhelminth type, branched and ending in flame cells, which are in *D. gyrociliatus* (according to Ed. Meyer, quoted by Lang) metamerically arranged, with a pair of external apertures to each segment. These facts taken together appear to me to do away with many of the difficulties urged by Bergh against the comparison of the Platyhelminth and Annelid excretory system.

A difficulty in comparing the Platyhelminth with the Annelid excretory system is undoubtedly in certain structural differences; there is no trace in any Platyhelminth of a "funnel;" the excretory tubules end in the well-known "flame cells." This difficulty has led Lang (11) to regard the funnel in the Annelid as a new structure unrepresented in the Platyhelminths; this opinion is supported by the observations

<sup>1</sup> Vejdovsky (13), pl. XVI, fig. 6.

of E. Meyer and of Vejdovsky (13), that in Polychæta and Oligochæta the funnel is developed perfectly independently of the rest of the nephridium. It was important, however, to note that not only is the nephridial funnel formed by the proliferation of a single cell, but that in Stylaria this cell becomes ciliated and acquires a lumen before it undergoes division; repeating in fact the presumed ancestral condition. With regard to the presence of a single flagellum in the "flame cells," Hartog has recently pointed out (10 A) that the optical effect produced by the motion of minute cilia might readily give the impression of a single flagellum. In the adult Clepsine (Bourne 5) the funnel consists of only two cells, so that it is but a stage removed from the Platyhelminth funnel. The above facts lend at least some support to the views that it is unnecessary to regard the funnels of the Annelida as new structures.

The facts recorded in the present paper fit in very well with the supposition that the Annelid excretory system is directly traceable to that of the Platyhelminth; I shall suggest, however, a course of development rather different from that put forward by Lang.

Lang has pointed out that in certain Planarians a commencing metamerism (parallel with the commencing metamerism of the generative organs, &c.) is visible in the excretory system. Here and there "secondary" external orifices are formed through branches given off from the longitudinal trunks of either side; at first irregular, these secondary pores finally become regularly disposed, and a paired arrangement even is seen; the disappearance of at least the greater part of the network (and the development of internal funnels) brings about the conditions which occur in *Lanice conchilega*; in this Annelid, Meyer (11) and Cunningham (6) have shown that the longitudinal trunks connecting the nephridia of successive segments persist; Vejdovsky also (13) has figured traces of this same longitudinal duct in *Anachæta*; and Wilson has recently (16) been able to prove that the embryo *Lumbricus*, like the embryo *Criodrilus*, possesses a similar longitudinal

duct, one on each side of the body. Finally, the disappearance of the longitudinal duct leaves the paired nephridia of the majority of Annelids. The remarkable disposition of the nephridia of *Pontobdella*, described by Bourne (5), is different in that there is not a single longitudinal duct on each side, but a continuous network. It resembles, in fact, as Lang has pointed out, the branched and anastomosing canals of the Trematode nephridium; it must also be remembered that the longitudinal canals of *Gunda segmentata* break up here and there into a network of anastomosing canals. It is this condition which has been inherited by *Pontobdella*, and also by *Perichæta*; *Perichæta* appears to me to represent a more archaic structure than *Pontobdella* since the external pores are more numerous; in *Pontobdella* they have become reduced to a single pair in each somite. *Acanthodrilus multiporus* offers the next stage; here the nephridial network is not continuous from segment to segment, but there is a separate network for each segment opening by numerous external pores. The Capitellidæ (Eisig 7) agree in many particulars with *Acanthodrilus*; the nephridia of each segment are numerous, and occasionally are connected; the ducts opening on to the exterior are often (Fischer 8) branched and open by several distinct pores. In the posterior region of the body of *Acanthodrilus* the external apertures are fewer, and are more particularly connected with the setæ, while the nephridial network tends to become arranged in a series of tufts, corresponding in number to the setæ; finally, the nephridial network of each half of the segment is independent. From *Acanthodrilus* to *Lumbricus* there is a considerable gap, only very partially bridged over by such forms as *Plutellus* (Perrier 12), where the irregularity in the position of the nephridial pores is, perhaps, to be regarded as a last trace of the numerous nephridial pores of *Acanthodrilus* and *Perichæta*. The above considerations necessitate a further inquiry into the nature of the longitudinal canal in *Lanice*, &c.; if it be assumed that this latter is the homologue of the longitudinal canal in the Platyhelminths, it must follow that the



Annelida have been derived from at least two Platyhelminth ancestors, i.e. one with a pair of longitudinal ducts, and another with a network of ducts. This would not perhaps be an unreasonable supposition were it not for the fact, that in this case *Lumbricus* must have had a different origin from *Perichæta*. The nature of this longitudinal duct has been put in a fresh light by the observations of Wilson (16); according to this author it arises from the epiblast, and is therefore comparable to the archinephric duct of Vertebrates, to which the observations of several writers have concurred in assigning an epiblastic origin. Haddon has recently (10) ingeniously suggested how a continuous groove, into which the nephridia opened, may have been converted into a canal opening into the cloaca. But while in the Vertebrata it seems to be generally agreed that the nephridial tubules are of mesoblastic origin,<sup>1</sup> Wilson states, that in *Lumbricus* they are budded out from the longitudinal duct, and are therefore epiblastic, with the exception of the funnel, which is mesoblastic. In any case his investigations only relate to early stages; and there is therefore nothing to negative the supposition that the portion which arises from the longitudinal duct is the vesicular region of the adult nephridium, which is known to be epiblastic, while the rest is mesoblastic.

Lang (11) dwells upon the identity of the longitudinal duct of Annelids with the longitudinal canals of Platyhelminths, but apparently in the belief that the former is of mesoblastic origin like the latter. There are, however, now considerable reasons for believing that the longitudinal duct of *Lumbricus*, and possibly of *Lanice*, is epiblastic; this homology cannot therefore be at present definitely accepted.

In the meantime, therefore, I would submit (1) that the origin of the Annelid excretory system from that of the Platyhelminths is as has been suggested in the present paper, (2) that the longitudinal duct of *Lumbricus*, *Lanice*, &c., has not any relation to that of the Platyhelminths.

<sup>1</sup> The pronephros has been described as formed by outgrowths of the archinephric duct, and therefore epiblastic.

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## EXPLANATION OF PLATES XXX and XXXI,

Illustrating Mr. Frank E. Beddard's paper "On the Occurrence of Numerous Nephridia in the same Segment in Certain Earthworms, and on the Relationship between the Excretory System in the Annelida and in the Platyhelminths."

## PLATE XXX.

FIGS. 1—6.—*Acanthodrilus multiporus*.

Fig. 1. Transverse section through body wall of 8th segment. *o*. External orifice of nephridium. *b*. Nephridium branching in the body wall and opening by several (three) orifices.

Fig. 2. Transverse section of one half of circumference of body wall of one of post-clitellar segments. *s*. Setæ. *n*. Nerve-cord. *p*. Peritoneum. *a*, *b*. Nephridial tubes.

Fig. 3. Similar section of a neighbouring segment; lettering as in last figure.

Fig. 4. Highly magnified section to show the course of a single nephridial tubule through the body wall. *ep*. Epidermis. *m*. Circular. *m'*. Longitudinal muscles. *p*. Peritoneum. *c*. Connective tissue. *a*, *b*. Nephridial tube.

Fig. 5.—Highly magnified section to illustrate the course of a nephridial tube within the substance of the peritoneum. Lettering as in last figure.

Fig. 6. Section through a single nephridial tube passing through the body wall. *a*, *b*. Nephridium. Other letters as in Fig. 4.

FIGS. 7—11.—*Perichæta aspergillum*.

Fig. 7. Longitudinal section through part of two adjacent segments. *cp*. Spermatheca. *n*. Nephridia. *s*. Intersegmental septum. Other letters as in Fig. 4.

Fig. 8. Transverse section of nephridiopore, highly magnified. *n*. Nephridium. Other letters as in Fig. 4.

Fig. 9. Transverse section through a portion of the body wall to show the nephridiopores. *np*. Nephridiopores. *e*. Epidermis. *s*. Setæ.

Fig. 10. Section through a single nephridial tube, passing through the body wall. *bl*. Blood-vessels. Other letters as in Fig. 6.

Fig. 11. Section through a portion of nephridial tube, highly magnified. *bl.* Blood-vessel. *n.* Marks the boundary between the region of the nephridium with an intracellular duct and that with an intercellular duct.

## PLATE XXXI.

FIGS. 12—14.—*Perichæta aspergillum*.

Fig. 12. Diagram of the relations of the nephridiopores (*o*) to the setæ (*s*), as seen on a superficial view.

Fig. 13. Diagram of the nephridial network in several segments. *o.* Nephridiopores. *p.* Nephridial network. *s.* Intersegmental septa.

Fig. 14. Diagram to illustrate the disposition of the nephridia in a single segment as seen in transverse sections. *s.* Setæ. *o.* Nephridiopores.

FIG. 15.—*Acanthodrilus multiporus*.—A diagram corresponding to the last. *s.* Setæ. *n.* Nephridiopores.





## The Anatomy of the Madreporaria: IV.

By

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With Plates XXXII and XXXIII.

As was pointed out in a former paper ("Anat. Madrep.," iii), the relations between the external body wall and the corallum of Madreporaria appear to yield a distinctive morphological character, and to depend upon the presence or absence of cœnenchyme. In all the genera yet examined in which the individual polyps are more or less free and independent of each other, the body wall is supported upon laminae of mesogloea and endoderm (generally termed the "peripheral lamellae"), which are continuous over the lip of the calyx with the mesenteries, and bear a constant relation to them. But in all the genera which form cœnenchyme, whether belonging to the Perforata or to the Imperforata, the body wall rests upon the little spikes or echinulations which stud the surface of the corallum. From this it would appear that a distinction, between forms with and without cœnenchyme, is justified by anatomical differences at least as great as those which differentiate Perforata from Imperforata; but our knowledge of the group is so slight that any generalisation such as the above is to be accepted with great caution. Of the 378 genera recognised by Professor P. Martin Duncan, in his recent "Revision of the Madreporaria" ('Journ. Linn. Soc. Zool.,' xvii), we have now a more or less complete account of the anatomy of only sixteen genera and a few more species, and the very foundations of a true morphology of the group have yet to be laid. Indeed,

the interest of some of the forms which I am about to describe lies in the fact that they exhibit a certain divergence from both the structural types mentioned above. An account of the following species will be found below.

Madracis asperula, p. 414.	Stephanaria planipora, p. 424.
Amphihelia ramea, p. 416.	Pocillopora nobilis, p. 425.
Stephanophyllia formosissima, p. 418.	Seriatopora tenuicornis, sp. n., p. 426.
Sphenotrochus rubescens, p. 421.	

### MADRACIS ASPERULA (fig. 1).

For the material for a study of this coral I am indebted to the courtesy of Mr. John Murray, who has placed in my hands the remainder of the spirit collection of Madreporaria obtained during the voyage of H.M.S. "Challenger."

In systematic position this coral is ranged by Martin Duncan close to the genus Stylophora, of the anatomy of which Dr. von Koch, of Darmstadt, has already published an account ('Jen. Zeitschr.,' xi). From this, however, *Madracis* differs in an important point.

The corallum, which requires here no systematic description, branches in digitate lobes, above the general surface of which the thecæ of the polyps project slightly. As in *Seriatopora*, *Stylophora*, and other such, it is Imperforate; the living tissues are confined to the external surface, and do not penetrate into the depth of the colony, the cavity formerly occupied by each polyp being shut off by a succession of "tabulæ" as growth proceeds.

The septa are eight in number, *Madracis* thus adding another to the several exceptions to Milne-Edwards' law, recently described. With this divergence, however, are not correlated in *Madreporaria* such marked structural differences as characterise the *Monauleæ*, *Edwardsiæ*, &c., which similarly diverge from Hexactinian symmetry. The septa are entocœlic only.

The polyps are in the main of Actinian structure; the body wall clothing the whole colony is composed of the ordi-

nary three layers. The tentacles are apparently both ecto-cœlic and entocœlic, and are simple evaginations tipped each by a single battery of nematocysts, as in *Seriatopora* ("Anat. Madr.," iii, fig. 11). The septa lie each between a pair of normal mesenteries. No differentiation of particular mesenteries is recognisable, and all extend to about the same depth into the polyp cavity. The two pairs of directive mesenteries are well marked, but it is worthy of note that the plane in which they lie does not always coincide with the axial-abaxial (dorso-ventral) plane which generally governs the orientation of similar colonies, but is here, in the case of some polyps, at right angles to it.

Madracis is of especial value as affording an intermediate condition between the two Madreporarian types mentioned above, in that the body wall is supported on the echinulations of the cœnenchyme only in certain more or less limited areas between the polyps, whereas immediately round the calyces are recognisable such peripheral lamellæ as are usually characteristic of forms devoid of cœnenchyme (fig. 1, B). This is probably due to the fact that the polyp calyces are slightly exsert above the general surface of the colony.

Here, therefore, we apparently have a condition morphologically intermediate between that of a solitary imperforate coral, as, for example, *Caryophyllia*, and such a cœnenchymatous form as *Seriatopora*. The condition in *Caryophyllia* (von Koch, 'Morph. Jahrb.,' v, fig. 4) and other simple forms is probably the more primitive. The next stage in the series seems to be indicated by the existing condition of *Lophobelia prolifera* ("Anat. Madrep.," iii, fig. 6), where the polyps and calyces are free and independent of each other, although a colony is formed by gemmation. Next it would appear that, as cœnenchyme was developed (presumably in order to increase the solidity and mass of the colony), and the spaces between the various polyps of the colony filled gradually with coral from below upwards, the peripheral lamellæ, as being necessarily confined to the immediate neighbourhood of the calyces, would be inadequate to bridge over the intercalated areas of cœnen-



chyme, and hence a new means of support for the body wall, namely, by means of the echinulations of the cœnenchyme itself, became necessary. The acquirement of this secondary condition is apparently represented by *Madracis*; but as the calyces are still slightly exsert above the cœnenchyme, the peripheral lamellæ are retained in the arææ immediately round the polyps. Lastly, in *Seriatopora* ("Anat. Madrep.," iii, fig. 9), which may represent the final term of the series, the calyces are merged in cœnenchyme, and no trace of the peripheral lamellæ is to be found.

As in other cœnenchymatous forms, by fusion of the body wall with the echinulations, the section of the cœlenteron lying below it is broken up into canals which form the only communication between the various polyp cavities.

A figure and description of the corallum may be found in Milne-Edwards and Haime, 'Ann. Sci. Nat.' (3) xiii, p. 101, pl. iv, fig. 2.

#### AMPHIHELIA RAMEA (figs. 2, 3).

Some specimens of the live coral were dredged off Lervik in Norway, by Professor E. Ray Lankester, who has been kind enough to entrust them to me for investigation.

Like *Lophohelia*, this genus forms by gemmation a branching colony without any development of cœnenchyme, the separate polyps being practically independent of each other. The theca is thin and imperforate, and marked externally by irregular longitudinal ridges and furrows which are of some morphological interest. The septa are generally twenty-four to twenty-eight in number, of which twelve to fourteen are smaller and ectocœlic, while a similar number are large and entocœlic. The latter unite below into a loose and irregular columella.

The body wall, which is composed of the usual three layers, forms a continuous sheet over the whole colony, and this, with a canal system to be shortly described, constitutes the sole connection between the adult polyps; that is to say, there is no continuity between the mesenteries of any given

polyp and those of its parent polyp below, though such a connection might have been expected. The tentacles are apparently both ectocœlic and entocœlic; but in these, as in other spirit specimens, it is difficult to determine the point with certainty. They are covered with batteries of nematocysts, as in *Flabellum* ("Anat. Madr.," i, fig. 9) and others. The mouth disc and stomodæum are normal, the lumen of the latter being nearly filled with coils of craspedon or the contorted edge of the mesentery. The mesenteries are generally in twelve to fourteen pairs of normal appearance, and in my specimens bore abundant ova. Unlike the condition recently described in *Lophohelia* ("Anat. Madr.," iii), there are present two pairs of well-developed "directive" mesenteries; the more remarkable as these two genera are most closely allied, and gemmation is of a similar character in both cases. All the mesenteries extend downwards nearly to the parent polyp, but do not touch it.

The most interesting point in the anatomy of *Amphihelia* lies in the relation existing between the external body wall and the corallum. For a very short distance round the lip of the calyx are recognisable, as in other free forms previously described, the characteristic peripheral lamellæ of the mesenteries (fig. 2, A). Just below the lip, however, the coral grows outwards at the points to which these lamellæ are attached, and the mesogloea lamina of the body wall comes to lie at these points directly on the broad ridges of coral thus formed (fig. 2, B). A series of canals lined by endoderm is left between these ridges, which are continuous over the lip of the calyx with the cœlenteron. These canals (fig. 3) are, in the main, parallel to the longer axis of the polyp, but are also connected by transverse branches; they come to lie in about the same radius as the mesenteries, and are generally equal to them in number, but are very irregular, both in position and formation. Like the body wall which bounds them peripherally, they appear to be continuous with the similar canals of the polyps above and below.

An examination of the corallum shows that the ridges be-

tween which the canals lie are not homologous with true costæ, since the latter (which are generally regarded as the ends of the septa, projecting radially outwards beyond the theca) are also represented round the lip of *Amphihelia*. They may perhaps bear some relation to the echinulations of cœnenchymatous forms; but here, as in most questions of Madreporarian morphology, a close investigation of a large number of allied forms is necessary for a true explanation of structure.

A figure and description of the corallum may be found in Milne-Edwards and Haime in 'Ann. Sci. Nat.' (3) xiii, p. 86, pl. iv, fig. 3.

#### STEPHANOPHYLLIA FORMOSISSIMA (figs. 4, 5, 6).

Professor H. N. Moseley has kindly handed to me for further investigation part of a decalcified specimen of this polyp, of which he has already published a partial account in his monograph of the Deep-Sea Madreporaria obtained by the "Challenger" ("Chall." Rep. Zool. ii, p. 203, pl. xvi). Owing to the fragmentary nature of the material, I am unable to give a detailed account of the general anatomy, but it is still possible to make out some points of interest.

As is the case in *Fungia*, and in the embryo *Astroides* described by von Koch and Lacaze-Duthiers, the corallum is plano-convex, resting free and unattached upon its plane surface. The latter constitutes the theca, and from it the septa rise perpendicularly upwards. The theca consists of a large number of concentric and radial trabeculæ, and from the radial trabeculæ rise alternately a mesentery and a septum (fig. 4). The septa are thus both ectocœlic and entocœlic, and, like the concentric trabeculæ from which they spring, lie free in the cœlenteron, not touching the body wall. On the other hand, those radial trabeculæ to which the mesenteries are attached, lie directly on the basal body-wall, and are united with it just as are the ridges and spikes in *Amphihelia* and cœnenchymatous forms.

*Stephanophyllia* therefore appears to stand in much the same relation to the family Eupsammidæ, with which it is generally

classed, as does *Amphihelia* to its family the *Oculinidæ*; that is to say, it is possible that in the former, as certainly in the latter, the peripheral lamellæ, which are found in such allied genera as *Rhodopsammia* and *Lophohelia* respectively, have been obliterated and functionally replaced by a radial outgrowth of coral from their points of attachment. The trabeculæ of coral to which the mesenteries are attached are of course not in this genus any more than in *Amphihelia* to be regarded as true costæ, since they bear no relation to the septa, and are a simple outgrowth from the theca.

In several respects *Stephanophyllia* exhibits a resemblance to the *Fungia* recently described by Bourne ('Quart. Journ. Micr. Sci.' xxvii). The plano-convex shape of the corallum, and the correlated basal position of the theca are of course characteristic of both genera; besides this, a view of a complete mesentery shows that a few synapticulæ brace together the septa of this coral, and that between the synapticulæ the muscular pleatings of the mesogloæ are gathered into strong bundles in a very characteristic manner hitherto described only in *Fungia* (fig. 5). The histological appearance of the craspedon is also similar and characteristic in both forms. On the whole, *Stephanophyllia* appears to bring *Fungia* into closer relations with the *Eupsammidæ* than have been generally allowed. At the same time it is to be remembered that in *Fungia* the body wall is, at any rate partially, supported on peripheral lamellæ.

The tentacles are ectocœlic as well as entocœlic, and are covered with batteries of nematocysts. As has been pointed out in other forms, the nematocysts are of two kinds, of which the smaller alone are to be found in the tentacles. In the craspedon, however, the larger kind is of exceptional dimensions, measuring as much as .144 mm. by .012 mm.; while the smaller form is only .048 in length. A pair of directive mesenteries occurred in the small fragment used for transverse sections.



## ON SOME STRUCTURES PREVIOUSLY DESCRIBED AS CALICOBLASTIC.

The only other point of interest noticed in *Stephanophyllia* is a structure for the firmer attachment of the mesentery to the corallum, a structure which occurs in many other genera, though a different significance has been hitherto assigned to it. In *Flabellum alabastrum* it is especially well developed, and consists of a series of processes given off radially into the corallum by the mesoglaea lamina of the mesentery (fig. 7). These processes are generally laminated, presumably for a further increase of the surface of attachment, and are directed obliquely downwards. In transverse sections of decalcified specimens of *Flabellum* and similar forms they often appear as a layer of polygonal bodies, striated as a rule radially, and lying between the mesoglaea and the space occupied before decalcification by the corallum (fig. 8). Such bodies were recently described by W. L. Selater ('Proc. Zool. Soc.,' 1886) in an account of *Stephanotrochus Moseleyanus* as calicoblasts or coral-forming cells; but vertical sections, cut parallel to the broader plane of the mesentery, show that such an explanation is untenable. A calicoblast is ontogenetically derived from the basal ectoderm of the embryo, and presumably has the characters which we ordinarily associate with a cell. A layer of such calicoblasts, obviously true cells, may be recognised at the growing points of any coral. The structures in question, however, are merely offsets of the homogeneous mesoglaea of the mesentery, and possess neither nucleus nor cell wall; nor is the mesoglaea of the Anthozoa, itself a secretion, known to exhibit secretory activity. Again, these processes do not occur at the growing points of the corallum. On the other hand, as they are to be met with only in the neighbourhood of the lines of attachment of the mesenteries to the corallum, their position, as well as their shape and lamination, indicate that their function is to provide an increased surface for fixation of the mesentery, and a firmer fulcrum for the action of the powerful

retractor muscles. The reason that their occurrence has been hitherto overlooked is, that the mesogloea is stained only when the colouring matter, whether carmine or hæmatoxylin, is strong and diffuse; but I have now detected them in *Flabellum* (2 sp.), *Amphihelia*, *Seriatopora* (2 sp.), *Pocillopora* (2 sp.), *Stephanophyllia*, and *Sphenotrochus*: and Bourne has recently described their occurrence in *Mussa* ('Quart. Journ. Micr. Sci.,' xxviii).

Dr. von Heider, of Graz, who was the first to call attention to the existence of calicoblasts, describes in a recent account of *Dendrophyllia* ('Zeitschr. wiss. Zool.,' xliv) a structure which he regards as calicoblastic, in terms which apply exactly to a transverse section of these processes. His figures (pl. xxxi, figs. 9, 11) do not, however, clearly show whether the two structures are identical or not, though it seems probable that they are so, and that what he describes as needles of calcium carbonate inside the "cells," are the lines of lamination (cf. Bourne, 'Quart. Journ. Micr. Sci.,' xxviii, p. 25). It should be noticed, on the other hand, that he explicitly states that, in some at least of these so-called cells, a nucleus was present.

In *Stephanophyllia* these processes are to be found at the base of each mesentery, and form a band running down the sides of the radial trabecula to which the mesentery is attached; but their structure is not different from those occurring in *Flabellum* and other forms, and their position a natural consequence of the different position of the theca (fig. 6).

Figures and description of the corallum may be found in Moseley, "Chall." Rep. Zool., ii, p. 198, pls. iv, xiii, xvi.

#### SPHENOTROCHUS RUBESCENS (figs. 9—12).

A study of some fragments of this coral, entrusted to me by Professor Moseley, has produced one or two points of considerable interest, though, as with *Stephanophyllia*, the account is necessarily incomplete.

The corallum is not unlike that of *Flabellum*, near which

it is placed by Martin Duncan ('Journ. Linn. Soc.,' xvii). From the latter it differs, in that soft tissues are present on the outside of the theca. The septa are both ectocœlic and entocœlic, and to both sets correspond true costæ, which extend downwards for some distance over the external surface of the corallum.

As was suggested by Moseley ("Chall." Rep. Zool., ii, p. 159), in complete retraction the tentacles are covered over by the mouth-disc, which is drawn inwards by a strong sphincter muscle (fig. 9). This constitutes the first recorded occurrence of "Rötteken's muscle" among Madreporaria; in longitudinal section it has the same "diffuse" appearance as that figured by the Brothers Hertwig, in *Sagartia parasitica* ('Jen. Zeitschr.,' xiii, pl. xix, fig. 18.) The mouth-disc itself is much corrugated, the rugæ consisting of lengthened columnar ectoderm cells supported by solid outgrowths of the mesoglœa, which is at this point very thick (fig. 10, A). The ectoderm of the tentacles consists almost entirely of nematocysts, showing but slight arrangement into batteries. The tentacles are apparently entocœlic only. The mesenteries appear to be normal, but in the fragment used for microscopic sections no directives were present. Both retractor (longitudinal) and protractor (oblique) muscles are exceptionally well developed, the former applied to such arborescent pleatings of mesoglœa as have been described among both Madreporaria and Hexactiniæ. It is worthy of note that there is so little cohesion between the muscle-fibres and the mesoglœa which affords them support, that they are frequently seen in transverse sections to tear away with the endoderm, leaving the mesoglœa bare. Over the whole of the polyp the mesoglœa is unusually strongly developed, and it exhibits at some points, the position of which appears to imply a more recent secretion than elsewhere, a great affinity for carmine, and a markedly vacuolated structure. The vacuoles are often empty, but contain, in many cases, brilliantly refractive crystals, the nature of which I was unable to ascertain. Cells are rarely to be seen in the mesoglœa. The processes for attachment of the mesentery to the corallum

(cf. p. 8, supra) are well developed, not only on the mesentery, but also on the thickened mesoglœa at the sides of the pseudocostæ (v. infra, and figs. 10, 11, *a*).

Encapsuled in the mesoglœa lamina of the mesentery and of its craspedon are numerous ova in various stages of maturation. So far as I am aware, all Anthozoan ova as yet described are formed in the endoderm, and then migrate into the mesoglœa, the latter forming a capsule appressed closely round them. In *Sphenotrochus*, however, the ovum is surrounded by a series of deeply staining bodies which lie between its membrane and the mesoglœal capsule (fig. 12). At first sight these corpuscles appear to consist of extruded yolk, but in most, if not in all, it is possible to detect a faint nucleus. Nearly triangular in section, their bases are pressed closely against the capsule, from which they sometimes shrink away, allowing their outline to be clearly seen. It is hardly possible to regard them as other than follicular cells. They are not present in the capsule of the smallest ovum observed ( $1 \times .07$  mm., diam. nucleus  $.008$  mm.), and their number increases up to a certain point with the size of the ovum. It is probable therefore that they migrate from time to time into the mesoglœa, as does the ovum itself; and their appearance indicates that their function may be to supply yolk-material for the ripening egg-cell. More deeply staining and larger bodies of irregular outline are found scattered in the endoderm of the craspedon, apparently identical with those described in *Euphyllia* (Bourne, 'Quart. Journ. Micr. Sci.,' xxviii, p. 31); these may bear some relation to the follicle cells.

The soft tissues external to the theca are also of some interest. No peripheral lamellæ of the mesenteries are recognisable, but at the points where they might be expected to occur are formed outgrowths of corallum comparable to those in *Amphihelia* (v. p. 5, supra.), on which the body wall rests (fig. 10, *B. a.*). The costæ corresponding to the entocœlic septa come also into direct contact with the body-wall (ibid., *a*<sup>1</sup>), while those of the entocœlic septa are free. At a lower level, however, both sets of costæ regularly serve for the



support of the body wall (fig. 11,  $a^1$ ), but here and there they fail to touch it (ibid.,  $a^2$ ), thus allowing of a cross communication between the longitudinal canals. The number of longitudinal canals is thus double that of the ectocœlic and entocœlic spaces, since the body wall is in contact both with true costæ and with pseudocostæ (i. e. those which replace the peripheral lamellæ). In the single perfect specimen of the corallum in the British Museum, the pseudocostæ are distinctly visible on the upper two thirds of the exterior of the calyx, but below this are lost in the true costæ. Unfortunately my fragments did not show the relations of the soft tissues in the lowest third.

Figures and a description of the corallum may be found in Moseley, "Chall." Rep. Zool., ii, p. 157, pl. vi.

#### STEPHANARIA PLANIPORA (fig. 13).

A specimen of a Psammocorid coral, for which I am again indebted to the generosity of Professor Moseley, appears to be identical with specimens of the above-named species in the British Museum. It is not recorded by Quelch ("Chall." Rep. Zool.), and therefore adds another to the "Challenger" species of Reef-corals. For the identification of this and many other corals, and for much other assistance, I desire to acknowledge my great obligation to Mr. Dendy, late of the British Museum.

The boundaries of the various polyps which compose the colony are so ill defined that it is impossible to decide how much of the soft parts seen in a transverse section should be referred to a particular individual. A glance at a figure of a section cut transversely to the axes of the polyps will show this (fig. 13). Each polyp possesses a stomatodæum, to which are attached a certain number of mesenteries, generally seven to ten; between these mesenteries lie entocœlic and ectocœlic septa, and over each entocœlic (?) septum is placed a tentacle of the simple character already described for Seriatopora, Madracis, &c. ("Anat. Madr.," iii, fig. 11). The muscles,

though obviously present, are not sufficiently developed to admit of a distinction of the mesenteries into pairs. The continuity of the mesenteries radiating outwards from the polyp is constantly broken by synapticulæ. The whole of the surface of the colony is practically composed of these radiating slips of mesentery lying between radiating septa, and interrupted by synapticulæ; and, except in the immediate neighbourhood of a polyp, it is often impossible to decide to which individual a mesentery is referable, since neither their direction nor musculature afford a clue. Contrary to what one might expect (cf. the more or less comparable condition in *Fungia*; Bourne, 'Quart. Journ. Micro. Sci.,' xxvii, pl. xxv, fig. 13), even such slips of mesentery as are at no point in contact with the stomatodæum often exhibit a filamentar (craspedal) thickening. Even at the uppermost ends of the branches, at a distance of perhaps a third of an inch from the nearest polyp, the same arrangement of mesenteries between septa (septo-costæ) is found. On these mesenteries the body wall is supported, although in places it appears to rest also on echinulations of the septa; as will be seen from the figure, there is practically no cœnenchyme. Through the inner parts of the colony ramifies a system of canals by which the various polyps are in communication with each other.

This genus appears to exhibit a distinct degeneration, implied by the low development of the mesenterial filament (a slight lengthening of the ordinary endoderm), and an individuality hardly more marked than in a Poriferan colony.

A figure and description of the corallum may be found in Verrill, 'Trans. Connect. Acad.,' i, p. 545, pl. ix, fig. 4.

#### POCILLOPORA NOBILIS.

For material of this species I am again indebted to Professor Moseley, who obtained it during the voyage of the "Challenger."

The anatomy agrees almost entirely with that of *P. brevicornis*, recently described ("Anat. Madr.," iii). The

differentiation of the mesenteries is similar, though perhaps hardly so well marked as in the other species, since the mesenteries numbered 3 and 10 in the diagram of *P. brevicornis* are often not appreciably longer than 5 and 8. The reticular tissue mentioned as filling in *Seriatopora subulata* and *P. brevicornis* the spaces from which corallum has been removed by decalcification, is in this species very much more clearly recognisable. It appears to consist of thin strands of (?) protoplasm (? mesoglœa), staining deeply with carmine; it retains the shape of the crystalline ellipsoids of which the corallum is ultimately composed, and forms an accurate cast of the dead internal parts of the colony.

*SERIATOPORA TENUICORNIS*, sp. n. (figs. 14, 15).

For a small fragment of a colony of this species I owe my thanks to Dr. S. J. Hickson, who collected it with other corals in the Celebes group.

In anatomy this form agrees exactly with the *Seriatopora subulata*, already described ("Anat. Madr.," iii). It appears to constitute a new species, of which the following are the diagnostic characters:—The branches are thin and finely tapering, exhibiting no tendency to unite in the manner characteristic of most *Seriatopora*; they are very solid in section, and bear four or five rows of calyces. The cœnenchyme is very regularly ribbed, the echinulations of which the ribs are composed being markedly short and blunt. The calyces project slightly above the surface of the cœnenchyme; the septa are generally about ten in number, short, and very irregular. The columella does not reach to the surface of the calyx; it is spinous, and not so plate-like as in some other species of the genus.

From *S. caliendrum*, to which it is approximate, it differs in that the calyces are farther apart, and project more from the cœnenchyme than in that genus; the echinulations are further apart, blunter, and shorter; the branches more slender. The specimen has been deposited in the British Museum.

## CONCLUSIONS.

The most important morphological points elucidated by a study of the species above described are as follows :

1. The apparent law that the body wall, when present, is supported in acœnenchymatous forms upon "peripheral lamellæ" of the mesenteries, and in cœnenchymatous species upon the echinulations of the cœnenchyme, is seen to require modification. The two methods of support may coexist in a cœnenchymatous form (*Madracis*), and to a certain extent in an acœnenchymatous species (*Amphihelia*); further, the body wall in acœnenchymatous species may rest upon pseudocostæ (? homologous with echinulations), either mainly (*Amphihelia*) or entirely (*Stephanophyllia*); or upon both pseudocostæ and true costæ (*Sphenotrochus*). At the same time it is doubtful whether such exceptions to the law, formulated above, will not eventually prove to be modifications due to exceptional conditions, of which we are at present ignorant.

2. The modifications of the mesenteries exhibited by previously described species of *Seriatopora* and *Pocillopora* are seen to extend to other species of the same genus.

3. The ultimate attachment of polyp to corallum consists, in many genera, in a series of laminated offsets of mesogloea in the neighbourhood of the mesentery, such structures having been previously described as calicoblastic in function.

4. A sphincter muscle, comparable to the "Rötteken's muscle" of *Hexactiniae*, may occur among *Madreporaria* (*Sphenotrochus*).

5. Follicle cells, which are perhaps immigrants from the endoderm, may surround the ripening ovum as it lies in its mesogloéal capsule (*Sphenotrochus*).

6. A case of degradation, tending to obscure the individuality of the polyps, is presented by *Stephanaria*.



## LIST OF THE PAPERS CHIEFLY QUOTED.

- BOURNE, G. C.—'Quart. Journ. Micr. Sci.,' xxvii (Fungia).  
 BOURNE, G. C.—'Quart. Journ. Micr. Sci.,' xxviii (Euphyllia, Mussa).  
 DUNCAN, P. M.—'Journ. Linn. Soc.," xvii (revision of genera).  
 FOWLER, G. H.—"Anat. Madr.," i, 'Quart. Journ. Micr. Sci.,' xxv; ii, *ibid.*, xxvii; iii, *ibid.*, xxviii.  
 VON HEIDER, A.—'Zeitschr. wiss. Zool.,' xlv (Dendrophyllia).  
 VON KOCH, G.—'Jen. Zeitschr. Naturw.,' xi (Stylophora).  
 VON KOCH, G.—'Morph. Jahrb.,' v (Caryophyllia).  
 MOSELEY, H. N.—"Chall." Rep. Zool., ii (Stephanophyllia, Sphenotrochus).  
 SCLATER, W. L.—'Proc. Zool. Soc.,' 1886 (Stephanotrochus).

## EXPLANATION OF PLATES XXXII and XXXIII,

Illustrating Mr. G. Herbert Fowler's paper on "The Anatomy of the Madreporaria," IV.

FIG. 1. MADRACIS ASPERULA.—Diagrammatic transverse section through a polyp at three different levels, showing the eight entocœlic septa and eight pairs of mesenteries. *A*, above the level of the theca; the exsert edges of the septa only are cut in this section. *B*, through the theca; showing the peripheral lamellæ. *C*, below the surface of the cœnenchyme. The support of the body wall on the echinulations agrees essentially with that of other forms previously figured (cf. "Anat. Madrep.," ii, fig. 4; or iii, figs. 2, 9). *d*., "directive" septa. *col.* Columella. *cœn.* Cœnenchyme. Ectoderm, "blocked" black and white; mesogloea, black; endoderm, grey; corallum, dotted (v. pp. 2—4).

FIG. 2. AMPHIHELIA RAMEA.—Diagrammatic transverse section through two quarters of a polyp, showing half of the twenty-four septa and of the twelve pairs of mesenteries. *A*, through the theca in the region of the tentacles, showing the peripheral lamellæ. *B*, below the stomodæum, showing the external canals between body wall and corallum. Ectoderm, quasi-cellular; endoderm, mesogloea, and corallum as in Fig. 1 (v. pp. 4—6).

FIG. 3. *AMPHIHELIA RAMEA*.—The body wall seen by transmitted light. The darker parts represent the canals, the lighter the ridges of coral between them.

FIG. 4. *STEPHANOPHYLLIA FORMOSISSIMA*.—Ideal diagrammatic representation of the relations of septa, mesenteries, costæ, and body wall to each other, in a small cube cut out from the base of the polyp. Ectoderm, "blocked" black and white; mesogloea, thick black line; endoderm, thin black line; corallum, dotted. Two radial trabeculæ (to which transparent mesenteries are attached) are cut across in the front part of the diagram, showing their connection with the body wall. From two other radial trabeculæ rise two septa, not touching the body wall at any point; of these septa the left-handmost is cut between two concentric trabeculæ, and the other at the point where concentric trabecula, radial trabecula, and septum meet. A synapticulum braces together the two septa, perforating the right-hand mesentery (v. p. 6).

FIG. 5. *STEPHANOPHYLLIA FORMOSISSIMA*.—View of a complete mesentery, with the basal (thecal) tissues attached. In the latter is seen the row of holes left by decalcification of the concentric trabeculæ; and in the mesentery four perforations produced by synapticulæ, at the sides of which the muscle plectings are gathered into characteristic bundles (v. p. 7).

FIG. 6. *STEPHANOPHYLLIA FORMOSISSIMA*.—Two transverse sections taken at the base of a mesentery. In *A*, the higher of the two, the concentric trabeculæ have cut the mesentery across, so that a series of plates resembling the one here drawn (*M*) is produced along the whole radius (cf. the condition in *Fungia*, Bourne, 'Quart. Journ. Micr. Sci.,' xxvii, Pl. XXV, fig. 13). In the plane of *B*, the section passes through a radial trabecula also, and is thus taken below the edge of the mesentery. In both sections are seen the processes for the firmer attachment of the mesentery (v. p. 8). The arrows indicate the direction of *R*., the radial, and *C*., the concentric trabeculæ.

FIG. 7. *FLABELLUM ALABASTRUM*.—Lateral view of the distal edge of the mesogloea lamina of a mesentery, i.e. of the edge which is attached directly to the corallum (cf. "Anat. Madrep.," i, fig. 2), showing the laminated processes of attachment of the mesentery (v. p. 8).

FIG. 8. *FLABELLUM ALABASTRUM*.—Transverse section of the base of a mesentery (*M*.), showing the processes of attachment lying in the space from which corallum has been removed. Those which are radially laminated are probably seen in transverse section, while parallel lamination indicates oblique section (cf. Selater, 'P. Z. S.,' 1886, pl. xiv, figs. 11—13).

FIG. 9. *SPHENOTROCHUS RUBESCENS*.—Transverse section through the sphincter muscle ("Röttiken's muscle"), which draws the mouth-disc over the tentacles.

FIG. 10. *SPHENOTROCHUS RUBESCENS*.—Transverse section (incomplete) through a pair of mesenteries and the surrounding tissues. Ectoderm and

endoderm, light grey; mesoglœa, dark gray; space formerly occupied by corallum, dotted. On each side of a central entocœlic septum lies a mesentery, external to which is an ectocœlic septum. Corresponding to the mesenteries are the pseudo-costæ (*a*) in direct contact with the body wall (*b. w.*), with which the ectocœlic costæ are also in contact (*a*<sup>1</sup>). The rugæ of the mouth-disc (*m. d.*) are seen in transverse section, supported on solid offsets of mesoglœa (v. pp. 9—12).

FIG. 11. SPHENOTROCHUS RUBESCENS.—Transverse section at a lower plane than is represented in Fig. 10, *A*. The body is in contact with pseudo-costæ (*a*), and with both ectocœlic and entocœlic costæ (*a*<sup>1</sup>). The latter, however, at certain points do not reach the body wall (*a*<sup>2</sup>), thus allowing of transverse communication between the longitudinal canals. (The theca has been diminished in breadth by one half.)

FIG. 12. SPHENOTROCHUS RUBESCENS.—Section through a portion of the ovum and surrounding tissues. The vacuolated ovum, bounded by a thin vitelline membrane, has shrunk in the preservative fluid away from the follicular cells. The latter lie closely appressed to the thin mesoglœal capsule, which is covered by endoderm cells externally (v. p. 11).

FIG. 13. STEPHANARIA PLANIPORA.—Section through a part of the colony at right angles to the polyps, of which three are included (*A, B, C*). The rest of the section is composed of the mesenteries and septa (septo-costæ) which radiate from them (v. p. 12).

FIGS. 14 and 15.—SERIATOPORA TENUICORNIS, sp. n. (v. p. 14). The drawings for these two figures are due to the skill of Miss Stone.

# A Monograph on the Species and Distribution of the Genus *Peripatus* (Guilding).

By

**Adam Sedgwick, M.A., F.R.S.,**  
Fellow of Trinity College, Cambridge.

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With Plates XXXIV to XL.

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## INTRODUCTION.

THE editors of the posthumous memoir of Professor F. M. Balfour on the anatomy and development of *Peripatus capensis* stated, in a note at the end of the memoir, their intention of preparing a complete monograph of the known species of *Peripatus*. This intention has at length been carried out, and the present monograph is the result of a laborious examination of all the specimens of *Peripatus* to which it has been possible to get access.

To my great regret Professor Moseley has been obliged, by his most unfortunate illness, to withdraw from active participation in the work; and the whole responsibility for the statements and descriptions falls upon me alone. But he has given me much valuable assistance, and has made some substantial contributions to the monograph. The most important of the latter relate to *Peripatus novæ-zealandiæ*. He examined this species with great care, and the drawings from which figs. 16, 17—20, and 30 were copied, were executed under his supervision.

The material at my disposal has been as follows:

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1. The material left by Professor Balfour. This comprised a large number of the Cape species collected by Mr. Lloyd Morgan and by the late Mr. Oakley of the South African Museum, and some specimens of the New Zealand species collected by Professor Moseley and Professor Jeffrey Parker. Balfour also had fourteen specimens from Caracas, sent him, I believe, by Professor Ernst, and one specimen from South Africa, of the exact locality of which I am ignorant, with twenty-two pairs of legs. This specimen was found by Mr. Mansel Weale, and given to Balfour by Mr. Wood Mason.

2. A large number of specimens from the Cape, collected partly by myself in 1883, and brought to England alive, and partly by Mr. C. Stewart, of the Royal Hotel, Wynberg, who in the winters of 1884-85 sent me a large additional supply of live animals collected on Table Mountain. I am under great obligations to Mr. Stewart, not only for these specimens, but for the great help which he gave me when I was at the Cape.

3. A large number of living specimens from Wellington, New Zealand. These are the only specimens of this species which have ever been brought to England alive, and I owe them to the kindness of two gentlemen, who were personally unknown to me until they began to help me in my *Peripatus* work. Mr. Noel Barraud, of Wellington, at the request of my friend Mr. G. E. Anson, M.A., of Trinity College, began to hunt for *Peripatus*, and was successful in finding them. His specimens were, after two unsuccessful attempts, brought to England alive by Mr. Edgar J. Evans, chief officer of the Shaw, Savill, Albion Company's magnificent steamer "*Tainui*." The first two lots all died soon after leaving Rio Janeiro, but in the third attempt Mr. Evans was successful in finding a place near the cold chamber, where the temperature in the tropics was not too high for the animals. Since the third attempt Mr. Evans has been successful every voyage. My most sincere thanks are owing to both of these gentlemen, who, though not specially interested in natural history, have put themselves to

very considerable trouble and inconvenience to satisfy what would have seemed to most people an absurd whim of a perfect stranger. The living animals brought by Mr. Evans have enabled me to give a much more complete account of the New Zealand species than if I had had to rely only on the somewhat shrunk and contracted specimens in Balfour's material; and the embryos found in them are now being used by Miss Sheldon (No. 45), of Newnham College, who is engaged in preparing a memoir of their development.

4. Several specimens of the neotropical group of species from the Museum of Copenhagen, most kindly sent to me by Professor Steenstrup, in response to the appeal for specimens at the end of Balfour's posthumous memoir.

5. Dr. J. Kennel, of Würzburg, was kind enough to send me, in exchange for two living specimens of *Capensis*, two specimens of the smaller species, which he found in Trinidad.

6. Four specimens from near Williamstown, South Africa, belonging to the Indian Museum.

7. All the specimens in the British Museum. These have not, unfortunately, been of so much use to me as I had hoped, on account of their small number and contracted condition, and of the difficulty of getting a sufficiently strong light in the rooms set apart for the examination of spirit specimens in the British Museum, for the minute examination which is required. I am greatly indebted to Professor Jeffrey Bell, of the British Museum, for his courtesy in giving me every facility in his power to examine the specimens.

8. Two specimens from Queensland, Australia, belonging to Professor Jeffrey Bell. He has been most kind in putting them entirely at my disposal for the purposes of this monograph.

9. About twenty specimens from Demerara, brought alive to England by Mr. W. L. Sclater. Mr. Sclater has himself given a short description of these specimens, and has kindly placed the greater number of them at my disposal for the purposes of this monograph. These specimens were all killed

and opened by me shortly after their arrival in order that their embryos might be cut out and preserved. The result is that they are somewhat contracted and not so favorable for observation as they would have been had they been drowned.

Of the figures illustrating this monograph, the beautiful drawings of *Capensis* on Pl. XXXV, of *Edwardsii*, *Moseleyi*, and *Novæ-zealandiæ* on Pl. XXXVII, were made by Miss A. B. Balfour in Professor Balfour's lifetime and under his direction. The figures on Pl. XXXVI were made by Miss Balfour after her brother's death. To enable me to complete the illustrations required and to assist in the publication of the monograph, the Government Grant Committee of the Royal Society granted the sum of £50. Figs. 16, 17—20, and 30 were made at Oxford by Mr. W. H. Hill, under Professor Moseley's direction and supervision. The remainder of the drawings, including that of the living animal of Pl. XXXIV, were made by Mr. E. Wilson, of the Cambridge Scientific Instrument Company. My best thanks are due to these gentlemen for the care and skill with which they have executed their work.

Finally, I have again to acknowledge my indebtedness to Professor Jeffrey Bell for his assistance in preparing the Bibliography. Several papers which had escaped my notice were first pointed out to me by him.

For an account of the general anatomy and characters of the genus *Peripatus*, I must refer to the memoirs of Moseley (No. 18), Balfour (No. 28), and Gaffron (Nos. 34, 35). In this monograph only those features of a specific differential value are dwelt upon. I have, however, made a partial exception to this rule in the case of *Capensis*, the external characters of which have been described at considerable length. The reader will be able to gather from this description a sufficient knowledge of the general external features of the genus to enable him to understand the short descriptions of the other species.

The chief result of my observations has been to establish a definite series of characters which distinguish quite sharply all the species found in one region of distribution from those found in the others. Excluding the doubtful case of the Sumatran species, *Peripatus* has been found in the Ethiopian region (South Africa), the Australasian, and the Neotropical regions, and in each of these regions the genus is represented by more than one species. I have been able to establish a certain number of new species, but on the whole I must confess to failure in this respect. My failure chiefly relates to the species from the Neotropical region, and is due to the insufficient number of specimens at my disposal. It is remarkable of the species from this region that the number of the walking legs varies considerably within the same species, and it is only possible to determine the limits of the variation by examining a large number of individuals. Inasmuch as the specific characters other than those afforded by the legs are extremely inconspicuous, the importance of having a large and well preserved material is obvious—large in numbers to enable one to establish the limits of leg variation, and well preserved that the more minute specific differences may be made out.

How inconspicuous the specific characters are is well shown by contrasting the South African species *Capensis* and *Balfouri*. That these are distinct species is proved by the fact that the number of legs is constant in all the large number of specimens examined, and by the fact that it is preserved in the reproduction of the species. Embryos removed from *P. capensis* have invariably seventeen pairs of legs, while embryos removed from *P. Balfouri* have invariably eighteen pairs. The other differences relate simply to the texture and tint of the skin, and are so minute as to escape any but the experienced eye.

Before concluding this introduction, I am desirous of pointing out how extremely loose and inaccurate have been the observations of some professed zoologists on the members of our genus. In several cases has it happened that the observer (*sit venia verbo*) has not been at the trouble of counting the



legs of his specimens, though he has not refrained from making statements on this point, and in more than one case the number of legs in the specimen figured does not correspond with the author's statement in the text. If one may draw conclusions as to these zoologists' ideas of accuracy in observation from such instances in which only the most obvious external features are concerned, one would be inclined to infer that but little value can be attached to their statements with regard to the more inconspicuous details, which require some nicety of observation.

### PERIPATUS, Guilding.

Soft-bodied vermiform animals, with one pair of ringed antennæ, one pair of jaws, one pair of oral papillæ, and a varying number of claw-bearing ambulatory legs. Dorsal surface arched and more darkly pigmented than the flat ventral surface. Skin transversely ridged and beset by wart-like spiniferous papillæ. Mouth anterior, ventral; anus posterior, terminal. Generative opening single, median, ventral, and posterior. One pair of simple eyes. Brain large, with two ventral hollow appendages; ventral cords widely divaricated, without distinct ganglia. Alimentary canal simple, uncoiled. Segmentally arranged, paired nephridia are present. Body cavity is continuous with the vascular system, and does not communicate with the paired nephridia. Heart tubular, with paired ostia. Respiration by means of tracheæ. Diœcious; males smaller and generally less numerous than females. Generative glands tubular, continuous with the ducts. Viviparous. Young born fully developed. They shun the light, and live in damp places beneath stones, leaves, and bark of rotten stumps. They eject when irritated a viscid fluid through openings at the apex of the oral papillæ.

Distribution: South Africa, New Zealand, and Australia, South America and the West Indies [and in Sumatra?].

The genus *Peripatus* was established in 1826 by Guilding (No. 1), who first obtained specimens of it from St. Vincent

in the Antilles. He regarded it as a Mollusc, being no doubt deceived by the slug-like appearance given by the antennæ. Specimens were subsequently obtained from other parts of the Neotropical region and from South Africa, and the animal was variously assigned by the zoologists of the day to the Annelida and Myriapoda (vide Moseley, No. 22, and Sclater, No. 41). Its true place in the system, as a primitive member of the group Arthropoda, was first established in 1874 by Moseley (No. 18), who discovered the tracheæ. It was reported from Australia in 1869 by Saenger (No. 15), and from New Zealand by Hutton (No. 19) in 1876. The nephridia were first discovered by Saenger (No. 15), but they were re-discovered and more fully described by Balfour (Nos. 21 and 28). Gaffron was the first to observe the cardiac ostia and the cilia in the generative tracts. The development has been worked at by Moseley (No. 18), Hutton (No. 19), Balfour (No. 28), and more in detail by Kennel (Nos. 32 and 33), Sheldon (No. 45), Sclater (No. 46), and myself (No. 39).

There can be no doubt that *Peripatus* is an Arthropod, for it possesses the following features, all characteristic of that group, and all of first-class morphological importance. (1) The presence of appendages modified as jaws. (2) The presence of paired lateral ostia perforating the wall of the heart and putting its cavity in communication with the pericardium. The importance of this feature as an Arthropod character was first pointed out by Lankester. (3) The presence of a vascular body cavity and pericardium (hæmocœlic body cavity). (4) The inconspicuous character of the cœlom in the adult. Finally, the tracheæ, though not characteristic of all the classes of the Arthropoda, are found nowhere outside that group, and constitute a very important additional reason for uniting *Peripatus* with it.

*Peripatus*, though indubitably an Arthropod, differs in such important respects from all the old-established Arthropod classes, that a special class, equivalent in rank to the others, and called *Prototracheata*, has had to be created for its sole occupancy. This unlikeness to other Arthropoda is mainly due to the Annelidan affinities which it presents, but in part

to the presence of the following peculiar features: (1) the number and diffusion of the tracheal apertures, (2) the restriction of the jaws to a single pair, (3) the disposition of the generative organs, (4) the texture of the skin, and (5) the simplicity and similarity of all the segments of the body behind the head.

The Annelidan affinities are superficially indicated in so marked a manner by the thinness of the cuticle, the dermo-muscular body wall, the hollow appendages, that, as already stated, many of the earlier zoologists who examined *Peripatus* placed it amongst the segmented worms; and the discovery that there is some solid morphological basis for this determination constitutes one of the most interesting points of the recent work on the genus. The Annelidan features are: (1) the paired nephridia in every segment of the body behind the first two (Saenger, Balfour), (2) the presence of cilia in the generative tracts (Gaffron). It is true that neither of these features are absolutely distinctive of the Annelida, but when taken in conjunction with the Annelid disposition of the chief systems of organs, viz. the central nervous system, and the main vascular trunk or heart, may be considered as indicating affinities in that direction. *Peripatus*, therefore, is zoologically of extreme interest from the fact that, though in the main Arthropodan, it possesses features which are possessed by no other Arthropod, and which connect it to the group to which the Arthropoda are in the general plan of their organisation most closely related. It must, therefore, according to our present lights, be regarded as a very primitive form; and this view of it is borne out by its extreme isolation at the present day. *Peripatus* stands absolutely alone as a kind of half-way animal between the Arthropoda and Annelida. There is no gradation of structure within the genus; the species are very limited in number, and in all of them the peculiar features above mentioned are equally sharply marked.

We may, therefore, with some justice, regard *Peripatus* as an animal which has persisted for a long time, with but little structural modifications; as the representative of an ancient

group, once widely diffused,<sup>1</sup> and probably rich in species and genera, and closely related to the ancestors of living Arthropoda. It probably has owed its preservation, as so many of the survivals of ancient types seem to have done, to the peculiar habits of life which are shared by all the living members of the class, viz. the habitual avoidance of the light of day, and the habit of seeking the obscurity and protection afforded by the spaces beneath stones and beneath the bark of trees.

*Peripatus*, though a lowly organised animal, and of remarkable sluggishness, with but slight development of the higher organs of sense, with eyes the only function of which is to enable it to avoid the light—though related to those animals most repulsive to the æsthetic sense of man, animals which crawl upon their bellies and spit at, or poison, their prey—is yet, strange to say, an animal of striking beauty. The exquisite sensitiveness and constantly changing form of the antennæ, the well-rounded plump body, the eyes set like small diamonds on the side of the head, the delicate feet, and, above all, the rich colouring and velvety texture of the skin, all combine to give these animals an aspect of quite exceptional beauty. Of all the species which I have seen alive, the most beautiful are the dark green individuals of *Capensis*, and the species which I have called *Balfouri*. These animals, so far as skin is concerned, are not surpassed in the animal kingdom. The drawing on Pl. I. is from one of the dark green specimens of *Capensis*. Clever as the drawing is, the artist has failed to catch the exquisite velvet of the skin; but this could hardly be expected in a lithograph. I never shall forget my astonishment and delight when on bearing away the bark of a rotten tree-stump in the forest on Table Mountain, I first came upon one of these animals in its natural haunts, or when Mr. Trimen showed me in confinement at the South African Museum a fine fat, full-grown female, accompanied by her large family of thirty or more just-born but pretty young, some of which were

<sup>1</sup> That the class had once a world-wide diffusion is indicated by the wide and discontinuous distribution of the living species.



luxuriously creeping about on the beautiful skin of their mother's back.

## THE SOUTH AFRICAN SPECIES OF PERIPATUS.

The following is a list of the distinct species of *Peripatus* which have so far been found in South Africa: *Capensis* (Table Mountain), *Balfouri* (Table Mountain), *brevis* (Table Mountain), *Moseleyi* (near Williamstown). In addition to these there are a certain number of other possible species, concerning the distinctness of which, however, I cannot be certain.

### General Characters of the South African *Peripatus*.

*Peripatus* with three spinous pads on the legs, with two primary papillæ on the anterior side of the foot (fig. 2), and a small tooth at the base of the main tooth on the outer blade of the jaw (fig. 28). The last fully developed leg of the males is provided with a white papilla on its ventral surface (fig. 4), and an enlarged crural gland. The generative opening is always subterminal and behind the last pair of fully developed legs. The ovaries are attached to the floor of the pericardium by a ligament which passes off from their front end. The terminal unpaired portion of the vas deferens of the male is short. The ova are large, but with little food-yolk. The portion of the proximal pad of the fourth and fifth legs, which carries the opening of the nephridium, is separated by faintly marked grooves from the rest of the pad (fig. 9). The legs appear, with rare doubtful exceptions, to be constant in number in all specimens of the same species. The median line of the dorsal surface is destitute of pigment.

*Peripatus capensis* being the best known and the most easily procured will be taken as the type of this group of species.

**Peripatus capensis.**

*South African Peripatus with seventeen pairs of claw-bearing ambulatory legs.*

The females are, on the whole, larger than the males, but the difference between them is not very marked. A large female would measure about 65 mm. ( $2\frac{1}{2}$  inches), and a large male about 48 mm. There are, however, other external differences between the sexes. The last leg of the male is smaller than the preceding, and rarely touches the ground when the animal is walking, while in the female it is as large as the others, and used in walking. Further, the last leg of the male possesses, on its ventral surface, a small white papilla (fig. 4), at the apex of which opens its crural gland, which is much enlarged.

In the living animal (Pl. I) the skin has a beautiful velvety texture. This is especially noticeable in the darker specimens.

**Colour.**—The colour varies in different individuals. But in general it may be said that the ventral surface has a light colour, and that the dorsal is darkly pigmented. The principal colours are two in number, which present every variation in tint in different individuals and in different parts of the body of the same individual. They are (1) a dark green, graduating to a bluish grey; (2) a brown, varying to a red orange.

The ventral surface is almost entirely free from the green pigment, but possesses a certain amount of light brown. This brown pigment is more conspicuous and of a darker shade on the spinous pads of the legs. The only part of the ventral surface where the green pigment is always present is the ventral side of the foot, where it has a blue tint, and round the lips (fig. 5). In the latter situation there are a number of green papillæ, with which are intermingled a few of an orange colour. Very rarely there is a suspicion of green pigment along the middle line of the ventral surface, and in one specimen I found the distal pad of the leg to contain green pigment.

While the colour of the ventral surface is practically the same in all individuals, that of the dorsal differs in almost all. The differences are due to the varying proportions in which the green and brown pigments are present.

To facilitate matters I will describe two extreme cases: (1) a very dark green specimen (fig. 1), in which the brown is very inconspicuous, and (2) a red specimen, in which the brown predominates.

(1) The skin between the close-set papillæ, so far as it can be observed, is a bluish grey; but on the papillæ the pigment has a very dark green colour, except on a few, in which it is brown (even these may be absent). The ground colour, i.e. the colour of the skin between the papillæ, varies in shade in different places. On the dorsal sides of the legs and along a dorso-lateral band at the bases of the legs, extending the whole length of the body, it is lighter than elsewhere, while on each side of the median dorsal white line it is much darker than elsewhere. These differences may be partly due to the closer aggregation of the papillæ in one place than in the other.

(2) The pigment of the skin and of most of the papillæ is a reddish brown, except on each side of the dorsal white line and on the dorsal sides of the legs where it is green. Scattered amongst the brown papillæ are a considerable number of green. The brown colour is of a lighter shade along a dorso-lateral band, extending the whole length of the body at the base of the legs, and from this band green papillæ are almost entirely absent. The brown pigment is, however, almost entirely absent from the dorsal side of the legs on each side of the dorsal white line.

The conditions intermediate between these two extreme cases are due to the variations in the number of the brown papillæ. As a peculiarity of these intermediate cases may be mentioned the fact that the brown pigment extends into the skin round the base of the brown papillæ, giving the brown papillæ a brown setting, so that when a number of them occur together the skin between the papillæ has an entirely brown colour (as in the brown specimens). Brown papillæ are most numerous in the light band at the bases of the legs, and are

sometimes so numerous that the ground colour in that region is brown, though green elsewhere on the back.

The pigment is always present, whether on the papillæ or between in minute square, pentagonal, and hexagonal patches. The darkness of the skin is probably mainly due to the number of these patches present in any given area.

The antennæ are always green, the brown being almost entirely absent from them, and they are the first to acquire the green colour in the embryo. In fact the young at birth are almost quite white excepting the antennæ.

The colour seems hardly at all affected by the action of spirit. The flesh-coloured brown of the ventral surface is sometimes slightly reddened when the animal is first put into spirit, but the red tinge soon vanishes, being apparently dissolved out by the spirit, which in such cases becomes slightly coloured.

**Ridges and Papillæ of the Skin.**—The skin is thrown into a number of transverse ridges, along which the primary wart-like papillæ are placed.

The papillæ, which are found everywhere, are especially developed on the dorsal surface, less so on the ventral. The papillæ round the lips differ from the remaining papillæ of the ventral surface in containing a green pigment. Each papilla bears at its extremity a well-marked spine.

The ridges of the skin are not continued across the dorsal middle line, being interrupted by the whitish line already mentioned. Those which lie in the same transverse line as the legs are not continued on to the latter, but stop at the junction of the latter with the body. All the others pass round to the ventral surface and are continued across the middle line; they do not, however, become continuous with the ridges of the other side, but passing between them gradually thin off and vanish. The ridges on the legs are directed transversely to the long axes of the legs, *i. e.* are at right angles to the ridges of the rest of the body.

The papillæ of the dorsal surface are not arranged in a single row in the ridges, but in more than one row, in fact a ridge varies in thickness in different parts of its course.



Further, the dorsal ridges are interrupted by thin and sharp, less coloured lines, which are somewhat diagonally arranged, and divide the ridges into lozenge-shaped areas (vide figs. 1 and 10).

**The antennæ** are ringed and taper slightly till near their termination, where they present a slight enlargement.

The rings consist essentially of a number of coalesced primary papillæ, and are, therefore, beset by a number of spines like those of the primary papillæ. They are more deeply pigmented than the rest of the antenna.

The free end of the antenna is covered by a cap of tissue like that of the rings. It is followed by four or more rings placed close together on the terminal enlargement. There appears to be about thirty rings on the antennæ of all adults of this species. But they are difficult to count, and a number of small rings occur, between them, which are not included in the thirty.

The antennæ are prolongations of the dorso-lateral parts of the anterior end of the body.

**The eyes** are paired and are situated at the roots of the antennæ on the dorso-lateral parts of the head. Each is placed on the side of a protuberance which is continued as the antenna, and each presents the appearance of a small crystalline ball inserted on the skin in this region.

The rings of papillæ on that part of the head from which the antennæ arise lose their transverse arrangement. They are arranged nearly concentrically to the antennal rings, and have a straight course forwards between the antennæ.

**The oral papillæ** are placed at the sides of the head. They are attached ventro-laterally on each side of the lips. The duct of the slime gland opens through their free end. They possess two main rings of projecting tissue, which are especially pigmented on the dorsal side; and their extremities are covered by papillæ irregularly arranged (vide description of oral papilla of New Zealand species, p. 29).

**The Buccal Cavity.**—The buccal cavity has the form of a fairly deep pit, of a longitudinal oval form, placed on the ventral surface of the head, and surrounded by a tumid lip.

The lip is covered by a soft skin, in which are numerous

organs of touch, similar to those in other parts of the skin, having their projecting portions enclosed in delicate spines formed by the cuticle. The skin of the lips is raised into a series of papilliform ridges, whose general form is shown in fig. 5; of these there is one unpaired and median behind, and a pair, differing somewhat in character from the remainder, in front, and there are, in addition, seven on each side. The cutaneous papillæ round the front of the lips are raised up and appear like a second outer lip concentric with the anterior part of the real lip, with the posterior part of which it is continuous.

The structures within the buccal cavity are shown as they appear in the surface views in fig. 5. In the median line of the buccal cavity in front is placed a thick muscular protuberance, which may perhaps conveniently be called the tongue, though attached to the dorsal instead of the ventral wall of the mouth. It has the form of an elongated ridge, which ends rather abruptly behind, becoming continuous with the dorsal wall of the pharynx. Its projecting edge is armed by a series of small teeth, which are thickenings of the chitinous covering prolonged from the surface of the body over the buccal cavity. Where the ridge becomes flatter behind, the row of teeth divides into two, with a shallow groove between them.

**The Jaws.**—On each side of the tongue are placed the jaws, which are a pair of appendages, modified in the characteristic arthropodan manner, to subserve mastication. They are essentially short papillæ, moved by an elaborate and powerful system of muscles, and armed at their free extremities by a pair of cutting blades or claws. The latter structures are, in all essential points, similar to the claws borne by the feet, and, like these, are formed as thickenings of the cuticle. They have, therefore, essentially the characters of the claws and jaws of the Arthropoda, and are wholly dissimilar to the setæ of Chætopoda. They are sickle-shaped, and, as shown in fig. 5, have their convex edge directed nearly straight forwards, and their concave or cutting edge pointed backwards. The inner cutting plate has five to eight teeth (fig. 27). The outer plate

has one main tooth (fig. 28), at the base of which is a small tooth. This accessory tooth is found on the outer blade in all South African species. Posteriorly, the behaviour of the two blades is very different. The epithelial ridge bearing the outer blade is continued back for a short distance behind the blade, but the cuticle covering it becomes very thin, and it forms a simple epithelial ridge placed parallel to the inner blade. The cuticle covering the epithelial ridge of the inner blade is, on the contrary, prolonged behind the blade itself as a thick rod, which, penetrating backwards along a deep pocket of the buccal epithelium, behind the main part of the buccal cavity for the whole length of the pharynx, forms a very powerful lever, on which a great part of the muscles connected with the jaws find their insertion.

**The Ambulatory Appendages.**—The claw-bearing legs are seventeen in number, and with the exception of the fourth and fifth pairs in both sexes, and the last in the male, they all resemble each other fairly closely. A typical appendage will be first described and the small variations found in the appendages just mentioned will then be pointed out. Each consists of two main divisions, a large proximal portion the leg, and a narrow dorsal, claw-bearing portion, the foot.

The **leg** has the form of a truncated cone, the broad end of which is attached to the ventro-lateral body wall, of which it appears to be, and is, a prolongation. It is marked by a number of rings of primary papillæ, placed transversely to the long axis of the leg, the dorsal of which contain a green and the ventral a brown pigment. These rings of papillæ at the attachment of the leg, gradually change their direction and merge into the body rings. At the narrow end of the cone there are three ventrally placed pads, in which the brown pigment is dark, and which are covered by a number of spines precisely resembling the spines of the primary papillæ. These spinous pads are continued dorsally, each into a ring of papillæ.

The papillæ of the ventral row next the proximal of these spinous pads are intermediate in character between the primary

papillæ and the spinous pads. Each of these papillæ is larger than a normal papilla, and bears several spines (fig. 2). This character of the papillæ of this row is even more marked in some of the anterior legs than in the one figured; it seems probable that the pads have been formed by the coalescence of several rows of papillæ on the ventral surface of the legs. On the outer and inner sides of these pads the spines are absent, and secondary papillæ only are present.

In the centre of the basal part of the ventral surface of the foot there is present a group of larger papillæ, which are of a slightly paler colour than the others. They are arranged so as to form a groove, directed transversely to the long axis of the body, and separated at its internal extremity by a median papilla from a deep pit which is placed at the point of junction of the body and leg. The whole structure has the appearance, when viewed with the naked eye, of a transverse slit placed at the base of the leg. The segmental organs open by the deep pit placed at the internal end of this structure. The exact arrangement of the papillæ round the outer part of the slit does not appear to be constant.

The **foot** is attached to the distal end of the leg. It is slightly narrower at its attached extremity than at its free end, which bears the two claws. The integument of the foot is covered with secondary papillæ, but spines and primary papillæ are absent, except at the points now to be described.

On each side of the middle ventral line of the proximal end of the foot is placed an elliptical elevation of the integument covered with spines. Attached to the proximal and outer end of this is a primary papilla. At the distal end of the ventral side of the foot on each side of the middle line is a group of inconspicuous pale elevations, bearing spines.

On the front side of the distal end of the foot, close to the socket in which the claws are placed, are two primary papillæ, one dorsal and the other ventral.

On the posterior side of the foot the dorsal of these only is present. The claws are sickle-shaped, and placed on papillæ on the terminal portion of the foot. The part of the



foot on which they are placed is especially retractile, and is generally found more or less telescoped into the proximal part (as in the figure).

The fourth and fifth pairs of legs exactly resemble the others, except in the fact that the proximal pad is broken up into three, a small central and two larger lateral. The enlarged segmental organs of these legs open on the small central division.

The last (17th) leg of the male (fig. 4) is characterised by possessing a well-marked white papilla on the ventral surface. This papilla, which presents a slit-like opening at its apex, is placed on the second row of papillæ, counting from the innermost pad, and slightly posterior to the axial line of the leg.

**The anal papillæ**, or as they should be called, generative papillæ, are placed one on each side of the generative aperture.

**The generative aperture** is subterminal and on the ventral surface. It is inconspicuous in most specimens.

**Internal Anatomy.**—The points of internal anatomy which require to be noted in an account of the species relate entirely to the generative organs. In the male the ductus ejaculatorius (posterior unpaired part of vas deferens, penis of Moseley) is short, and the crural glands of the seventeenth pair of legs are much elongated, reaching forward for a considerable distance in the lateral compartment of the body cavity.

In the female the ovaries are closely approximated and short. They are united to the floor of the pericardium by a single ligament passing off from their front end. Receptacula seminis are absent. The ova contain but little food-yolk. They are oval in shape, and the greatest length of an unsegmented ovum which has passed into the oviduct is .56 to 6 mm.

**Habits.**—They live beneath the bark and in the crevices of rotten stumps of trees, and beneath stones. So far they have only been found, so far as I can ascertain, in the woods on the slope of Table Mountain. They require a moist atmo-

sphere, and are exceedingly susceptible to drought. They avoid light, and are therefore rarely seen, and it is owing to this fact that, though fairly numerous, they were for so long unknown to the inhabitants of the Cape Peninsula. They move with great deliberation, picking their course by means of their antennæ and eyes. It is by the former that they acquire a knowledge of the ground over which they are travelling, and by the latter that they avoid the light. The antennæ are extraordinarily sensitive, and so delicate indeed, that they seem to be able to perceive the nature of objects without actual contact. When irritated they eject with considerable force the contents of their slime reservoirs. The force is supplied by the sudden contraction of the muscular body wall. They can squirt the slime to the distance of almost a foot. The slime, which appears to be perfectly harmless, is extremely sticky, but it easily comes away from the skin of the animal itself.

I have never seen them use their apparatus for the capture of prey. So far as I can judge it is used as a defensive weapon; but this of course will not exclude its offensive use. They will turn their heads to any part of the body which is being irritated and violently discharge their slime at the offending object. Locomotion is effected entirely by means of the legs, with the body fully extended.

Of their food in the natural state we know nothing; but it is probably mainly, if not entirely, animal. Those which I kept in cavity eagerly devoured the entrails of their fellows, and the developing young from the uterus. They also like raw sheep's liver. They move their mouths in a suctorial manner, tearing the food with their jaws. They have the power of extruding their jaws from the mouth, and of working them alternately backwards or forwards. This is readily observed in individuals immersed in water.

The young are born in April and May. They are almost colourless at birth, excepting the antennæ, which are green, and their length is 10 to 15 mm. A large female will produce thirty to forty young in one year. The period of gestation is

thirteen months, that is to say, the ova pass into the oviducts about one month before the young of the preceding year are born. They are born one by one, and it takes some time for a female to get rid of her whole stock of embryos; in fact, the embryos in any given female differ slightly in age, those next the oviduct being a little older (a few hours) than those next the vagina.

The mother does not appear to pay any special attention to her young, which wander away and get their own food.

There does not appear to be any true copulation. The male deposits small, white, oval spermatophores, which consist of small bundles of spermatozoa cemented together by some glutinous substance, indiscriminately on any part of the body of the female. Such spermatophores are found on the bodies of both males and females from July to January, but they appear to be most numerous in our autumn.

The testes are active from June to the following March. From March to June the vesiculæ of the male are empty.

### **Peripatus Balfouri** (n. sp.).

*South African Peripatus, with eighteen<sup>1</sup> pairs of claw-bearing ambulatory legs, of which the last pair is rudimentary, with white papillæ on the dorsal surface.*

*Peripatus Balfouri* resembles very closely *P. capensis*. The points of difference are as follows:

The dorsal skin has an olive-green tinge. The largest papillæ are white, except at their free extremities, which are green (fig. 10). The white spreads out a little round the base of the papillæ. Brown tints are entirely absent in all the specimens which I have examined except one.

The ventral surface is whiter than in *Capensis*, but the papillæ are faintly green. The same remark applies to the ventral surface of the legs.

**The Ambulatory Appendages.**—The claw-bearing legs are eighteen pairs. The legs of the eighteenth pair are smaller

<sup>1</sup> Peters (No. 25) states that there are in the Berlin Museum specimens from the Cape with eighteen pairs of legs (see p. 25).

than the rest (fig. 24). The remaining ambulatory appendages resemble, except in the following points, those of *Capensis*. The three spinous pads are green, and the middle one is broader than the other two; the ventral surface of the proximal part of the leg is white, and the papillæ are a bluish green; the groove at the base is less marked than in *Capensis*.

The foot is rather more delicate than in *Capensis*, and the spines on the ventral side of the base of the claws are placed on two pairs of small papillæ (fig. 9).

The male is distinguished from the female, as in *Capensis*, by the possession of a white papilla on the ventral side of the legs of the seventeenth pair, in the same position as in *Capensis*, and the legs of the eighteenth pair are smaller than in the female. So small are they, indeed, that they are hardly distinguishable from the large papillæ found near the hind end of the body; but they bear two claws, and a rudiment of the foot may be made out.

In the female the legs of the eighteenth pair (fig. 24) present the following features:—The foot seems to be normal and unreduced, but the leg is much reduced, presenting on the ventral side only three rows of papillæ and one spinous pad, which indeed shows, in some specimens more than others, its constitution of separate papillæ. The pad and papillæ are all tinged with green.

The embryos are much smaller than in *Capensis*. In preserved specimens the length of the fertilised ovum is .4 to .48 mm.; and a full sized adult specimen may reach the length of 43 mm. The generative orifice is between the rudimentary legs of the eighteenth pair. As a peculiarity in habits may be mentioned the fact that the individuals of this species nearly always coil themselves into a spiral when touched, while *Capensis* simply contracts and shortens itself.

Locality—Table Mountain.



### Other South African species.

In addition to these two South African species from Table Mountain, the following varieties, some of which at least are probably distinct species, are known.

1. One with fourteen pairs of legs, already named **P. brevis** (Blainville). This species was found by M. Goudot beneath a stone in the woods on Table Mountain. It has been shortly described by Blainville in a note on p. 38 of Gervais' "Études pour servir à l'histoire naturelle des Myriapodes" ('Ann. d. Sci. Nat.,' series ii, vol. vii) as follows:—"Corps subfusiform pourvu de quatorze paires de pattes, noir velouté en dessus, blanchâtre en dessous; longueur totale en comprenant les antennes, 43 mill.; plus grande largeur, 4 mill."

2. Another with nineteen pairs of legs,<sup>1</sup> reported by Mr. Roland Trimen from Plettenberg Bay, Cape Colony, but hitherto undescribed.

3. A third, in my possession, from Table Mountain with twenty pairs of claw-bearing legs, I have found one specimen only. Peters (No. 25) records the existence of specimens from the Cape with twenty pairs of legs (see below p. 455).

4. A fourth, with twenty-one<sup>1</sup> pairs of legs from near Williamstown, South Africa, I have only seen three specimens. They are in the possession of the Indian Museum.

5. A fifth, with twenty-two<sup>2</sup> pairs of legs, of which two specimens are known to me. One of these is in the possession of the Indian Museum; the locality is marked "near Williamstown, S. Africa." The other was found by Mr. J. P. Mansel Weale, and given by him to Mr. Wood Mason, who in his turn gave it to Professor Balfour. This specimen, of which I have not been able to ascertain the exact locality, is in my possession, and is figured on Pl. XXXVII fig. 8.

<sup>1</sup> There are specimens in the Berlin Museum with nineteen pairs of legs (Peters, No. 25).

<sup>2</sup> Peters (No. 25) records the existence of specimens from the Cape with twenty-one and twenty-two pairs of legs (see below, p. 455).

Of these five varieties I have not seen the first two. I have, however, had full opportunity of examining preserved specimens of the last three and will now shortly describe my observations on them.

**Peripatus with twenty pairs of claw-bearing legs.**—One specimen only—a female—is known to me. Locality, Table Mountain. Length of spirit specimen 23 mm.

The specimen very closely resembles *P. Balfouri*, and would be mistaken for the latter were not its legs counted. The skin presents an identical appearance. The last pair of legs are very small and rudimentary, and the generative opening, which is subterminal just in front of the anus, is between them.

The first nineteen pairs of legs are all normal and resemble exactly, so far as I can judge, those of *P. Balfouri*. In the legs of the twentieth pair, while the foot is normal the leg is much reduced in size. It is entirely without the spinous pads, and possesses only three rows of papillæ of which the row next the foot is slightly tinged with green, the other two being white.

The only other difference which I was able to detect between this specimen and *P. Balfouri* consisted in the very small amount of green on the ventral surface, which is almost white.

On the whole I am not inclined to establish at present a distinct species for the reception of this specimen, but would prefer to regard it provisionally as a variety of *P. Balfouri*.

### **Peripatus Moseleyi.**

*South African Peripatus, with twenty-one and twenty-two pairs of legs.*

All the specimens under this head presented the same general appearance (fig. 24). Were it not for the number of legs they would be taken for specimens of *Capensis*. The ventral surface is light brown and the dorsal an olive green, with scattered brown patches. Green is entirely absent from the ventral surface, excepting on the foot and distal pad, and sometimes a very little on the middle pad. On the dorsal surface there is a band on each side at the base of the legs, in

which the brown papillæ are so numerous as to cause the appearance of a brown band. Elsewhere on the dorsal surface the brown papillæ are very sparsely scattered.

They are all reported from a part of South Africa far removed from Table Mountain, the home of *Balfouri* and *Capensis*, viz. near Williamstown (with the possible exception of the one figured, the locality of which I do not know). Unfortunately I have only been able to see preserved specimens, which, on account of the great contraction they had undergone in dying, were not very favorable for observation.<sup>1</sup>

*Specimens of Peripatus Moseleyi with twenty-one pairs of legs.*—Skin as in *Capensis*. *Foot* and *legs* as in *Capensis*. At the bases of some of the legs (no constancy in the different specimens), immediately internal to the opening of the segmental organ, a small white patch of a tumid appearance is present. It occupies the same position as the large tumid papillæ on the ventral side of the leg of *Capensis* (see Pl. XXXVI, fig. 2), and has been noticed by Wood Mason (No. 23). The generative opening is subterminal, and on each side of it there is an inconspicuous anal papilla. The dorsal side of the foot is marked with streaks of green pigment, arranged parallel to its long axis. The streaks are much less distinct on the anterior than on the posterior feet.

Two of the specimens were smaller than the third, from which they differed by possessing a distinct white papilla on the last (twenty-first) leg, exactly resembling in appearance and position the papilla on the last leg of *Capensis*. I opened one of these smaller specimens, and found it to be a male; while the larger specimen turned out to be a female.

The female was about 26 mm. in length, the male about 20 mm.

*The specimens of P. Moseleyi with twenty-two pairs of legs* were both females. They resemble the specimens with twenty-one legs, so far as I could see from a study of the contracted

<sup>1</sup> Drowning (twenty-four hours or more) and then spirit is the best method of killing *Peripatus* for museum purposes and observation of external characters.

specimens at my disposal, except in two points: (1) in the absence of the anal papillæ, and (2) in the fact that the streaks on the dorsal side of the feet were entirely absent in the first nine pairs of legs. The legs of the last pair resemble, in all respects, the preceding, and the genital opening is behind them.

One of these specimens measured 26 mm. and the other 30 mm. in length.

Inasmuch as I have not been able to find any marked characters associated with the character afforded by the number of legs, and further, as I have had no opportunity of ascertaining whether the latter character is transmitted in reproduction, I am inclined not to establish two distinct species but to regard the specimens with twenty-two legs to be a variety of the species *Peripatus Moseleyi*, which is distinguished by the possession of twenty-one legs, and a subterminal genital opening behind the last legs.

Peters (No. 25) in a short paper on the variation of the number of legs in *P. capensis*, states that the following specimens were brought to him from Cape Town by a friend of his: three specimens with 22 legs, eight with 21, eight with 20, one with 19, one with 18, and two with 17 legs. He adds that they were all found in the same locality, which, however, is not mentioned. He gives no description of the specimens, beyond mentioning the number of legs, and it is not therefore possible to say whether he is right or not in his view that they all belong to the species *Capensis*. I may add that, though I have examined more than a thousand specimens from the Cape Peninsula, I have only seen one specimen with more than eighteen pairs of legs.



## THE AUSTRALASIAN SPECIES.

## GENERAL CHARACTERS.

*Peripatus* with fifteen pairs of claw-bearing ambulatory legs, with three spinous pads on the legs, and a primary papilla projecting from the median dorsal portion of the foot (figs. 21, 21a). The ventral organs are conspicuous, and the males are considerably smaller than the females. The generative opening is between the legs of the last pair, and there are no anal papillæ. The number of legs are constant in all specimens. The ovaries are attached by their whole length to the floor of the pericardium, and each oviduct is provided with a receptaculum seminis. The unpaired portion of the vas deferens is long and complicated in structure. The ova are large and heavily charged with food yolk. The portion of the proximal pad of the fourth and fifth legs which carries the opening of the nephridium is continuous distally with the rest of the pad (fig. 21). A median dorsal white line is present.

Two species are known from the Australasian region; *P. novæ-zealandiæ* from New Zealand, and *P. Leuckarti* from Queensland in Australia.

The former was first described by Captain Hutton (No. 19), the latter by Saenger (No. 15).

***Peripatus Novæ-Zealandiæ.***

(Figs. 7 and 17.)

*Australasian Peripatus, without a small tooth at the base of the main tooth of the outer blade of the jaw, and without a white papilla on the ventral side of the last leg of the male.*

The males are considerably smaller and less numerous than the females. The length of a large female is 50 mm. (2 inches), that of a large male 25 to 30 mm. in the extended condition after drowning. There is no external difference which enables us to distinguish the sexes. The ventral organs, owing to the

character of their pigment, are much more conspicuous than in the South African species.

**Colour.**—The colour varies in different individuals (*c.f.* figs. 7 and 17). The ground colour varies exceedingly in tint; it consists of a bluish grey, or slate colour, or violet; it is darker on the antennæ than elsewhere, and is especially concentrated in small, dark, square, pentagonal, and hexagonal patches lying close together over the whole surface of the body. Sometimes the outline of these patches is darker than the centre.

The pigment of the papillæ is also much darkened, but this requires a separate description as the variations in the colour of different individuals is mainly due to the papillæ. In all specimens a certain number of the papillæ have brown or orange pigment, which spreads out for a short distance around the base of the papilla, as in the case of the white papillæ of the South African *Peripatus Balfouri*, so that if many of these papillæ occur close together the ground colour is brown or orange and the slate entirely displaced; if such are numerous, they impart a distinctly brown aspect to the specimen. They are scattered irregularly over the whole surface of the body, but are most numerous, as in *Capensis*, in two bands on the sides of the dorsal surface at the base of the legs, where, indeed, in some specimens they almost completely replace the blue.

In most specimens, however, the greater number of papillæ presents a pigment which resembles more or less closely that of the ground colour. In many specimens—perhaps the majority—the papillæ have a dark slate colour; but in some specimens they may have a distinctly blue pigment, and occasionally even a dark purple. The lips, as in *Capensis*, are always destitute of pigment, and, as in that species, there is a sharp line extending along the middle of the whole length of the dorsal surface, in which the pigment is either absent or of an extremely light shade. On each side of this line the pigment in the papillæ is much darkened. The pads of the legs vary much in colour. In most specimens the distal one is blue, the middle one brown or orange, and the proximal one brown or orange in the centre,

and blue along the outer and inner border. In some specimens, however, they are all blue, and in others all brown or orange. In short, it may be said that the colour of the pad varies from blue with hardly any admixture of brown, to brown or orange without any blue. The distal pad is always the most blue. The row of composite large papillæ next to the proximal pad presents the predominant colour of the proximal pad. The blue colour is always absent from the ventral organs, which are either white, brown, or orange.

In all specimens there is a band of especially dark papillæ extending from the ventral extremity of the leg towards the ventral organ (fig. 19). The opening of the segmental organ is placed in the outer end of this band. The ventral surface is almost always mottled, the blue and yellow pigment being distributed in patches; the colour in each kind of patch extending between the papillæ as well as on to them.

**The ridges and papillæ of the skin** are arranged as in the South African species.

**The antennæ** resemble those of the South African species. They are ringed and slightly swollen near the free end (fig. 16). In none of the specimens that I examined did they present any brown pigment. They are entirely of the blue (violet?) grey colour, which forms the ground colour of the skin. The rings are beset with spines, and are covered by closely approximated patches of dark pigment such as have been already described. On the anterior edge of the rings at the front end of the antennæ there is a row of hexagonal, lighter-coloured spaces. At the bases of the spines also the pigment is lighter than elsewhere on the rings. Between the rings spines and patches are absent, and the pigment is of a lighter colour. The free end of the antenna is rounded and covered by a cap of integument resembling that on the rings and bearing a large number of spines, as in all the species of *Peripatus* that I have seen.

**The eyes** resemble in position and character (fig. 18) those of the South African species.

**The oral papillæ** resemble essentially those of *Capensis*.

Fig. 20 shows very clearly the peculiar collapsable joints which this appendage possesses in all the species.

**The buccal cavity, tongue, and lips** resemble in all respects the same structures in the South African species.

**The jaws** differ from those of the latter only in being without the small tooth on the outer blade.

**The ambulatory appendages** (fig. 21) are fifteen in number in all the specimens which I have examined. They resemble in their general features the same structures in *Capensis*, so that in the following short description stress will be laid only on the points in which they differ from the latter.

The opening of the segmental organ at the base of the leg is much more indistinct than in *Capensis*, and the peculiar tumid papillæ, which in *Capensis* extends from its outer border on to the ventral surface of the leg, are absent in this species. There are three pads, but the large papillæ of the row adjoining the proximal pad are larger with regard to the ordinary papillæ than in *Capensis*. Sometimes, indeed, they are so large as to present the appearance, unless closely examined, of one continuous spinous pad.

The foot differs from that of *Capensis* in the following points. The two prominent papillæ, placed one on each side (anterior and posterior) of the base of the foot are absent. The dorsal side of the foot near the free extremity possesses a papilla (fig. 21a), while the anterior face bears, like the posterior, only one papilla. As in *Capensis*, the opening of the nephridia of the fourth and fifth legs are placed on a small portion of the proximal pad. The part of the pad around the opening is only partly separated from the rest (vide fig. 21). The fifteenth leg, so far as I could ascertain, differs only in size (being slightly smaller) from the preceding, and is without the white papilla found on the last leg of the male of the South African species. Anal papillæ are never present.

**Internal Anatomy.**—As already explained, I do not propose to give in the monograph any detailed account of



internal structure. It will be sufficient for my purpose to sum up briefly the more striking differences between the various species.

The internal structure of *Peripatus novæ-zealandiæ* closely resembles that of the South African species. The differences, so far as I have been able to observe them, chiefly concern the generative organs, and the crural glands. It has recently been shown by Miss Sheldon (No. 40) that the crural glands are entirely absent from this species in both sexes.

The generative organs of the male differ from those of the Cape species in three points, viz. : (1) In the much greater length of the terminal unpaired portion of the vas deferens ; (2) in the absence of any specially enlarged crural glands in the last pair of legs ; (3) in the fact (recently shown by Miss Sheldon, No. 40), that the accessory glands, which are longer than in the male of *Capensis*, do not open with the vas deferens, but on the sides of the body outside the nerve-cord and close to the hind end. The terminal unpaired portion of the vas deferens is continuous with the two vasa deferentia (one of which passes as in *Capensis* beneath the two nerve-cords) at the level of the last pair of legs. Thence it is continued forwards for a considerable distance (as far as the level of the eighth legs in some cases) ; eventually bending round to pass backwards to its opening between the last pair of legs. Its walls increase in thickness from before backwards, and are of a distinctly gelatinous consistency in the greater part of their course.

The generative organs of the female differ from those of *Capensis* in two main points, viz. : (1) The two ovarian tubes are much longer, extending from the level of the eleventh to that of the thirteenth, and sometimes to that of the fourteenth leg, and are entirely separate from one another, each being suspended throughout its entire course to the pericardial floor by a distinct membrane. (2) There are two spherical receptacula seminis, each of which opens into the oviduct by two ducts ; and the oviduct in the neighbourhood of these openings is slightly sacculated.

It will be remembered that in the Cape species the ovarian

tubes were closely applied together and united to the pericardial floor only at their anterior extremities by a single band.

Spermatozoa have been found in the receptaculum and in the oviduct near the opening of the latter. There are few, if any, spermatozoa in the ovary. I have not been able to see, though I have examined live specimens with great care, a trace of cilia in any part of the female organs. It will be seen from the above that I take exception to Captain Hutton's<sup>1</sup> description of the ovary as an ovate organ.

The ova are large, oval in shape, and heavily charged with food-yolk. They are surrounded by a membrane of the same nature as the egg membrane of *P. capensis*, but much tougher. The greatest length of an unsegmented ovum from the uterus is about 1.5 mm., the breadth .8 mm. The greatest number of embryos found in one animal was eighteen, twelve in one uterus and six in the other. But the number varies in the different specimens. Captain Hutton found eighteen in one uterus and eight in the other. The same naturalist states that "when the embryos are numerous there is a considerable difference in the point of development to which they have attained." I can confirm this statement; but the greater number of the embryos in any given animal are of the same age.

**Habits.**—Captain Hutton (No. 19) has fully described the habits of this species. He says:

"They live in decayed wood, under stones, or in crevices of rock. They are nocturnal, but will feed in the daytime when hungry. They feed upon animals. I have seen one shoot out its viscid fluid from the oral papillæ at a fly introduced into the jar in which it was confined, and stick it down; it then went up and sucked its juices, rejecting the whole of the integument. This viscid fluid is for offensive and not defensive purposes. In the winter they become half torpid, though procreation still goes on. During this time of the year I have never seen them feed, and they cannot emit their viscid

<sup>1</sup> I have not been able to see any trace of the lateral vessel of Captain Hutton.

fluid, or only in very small quantity. They move with deliberation, entirely by means of their legs, the body being much lengthened. When walking, the antennæ are constantly moved about as feelers. If a needle is placed upright immediately in front of one, the antenna is drawn past it without actual contact; but the points of the hair probably touch the needle. Although viviparous, the eggs are often extruded before the development is complete, but these always die."

From the study of the living specimens brought by Mr. Evans I have been able to confirm Captain Hutton's observation as to the habits of the species, so far as it was possible to do so on imported specimens.

I have not been so fortunate as to see them catching flies with their slime, but this is not to be wondered at considering the greatly changed conditions in which I observed them. In fact I have failed to keep the specimens alive for any length of time in this country.

Having received two lots, one in July and the other in December, I am able to make some conjectures as to the period of gestation. Captain Hutton asserts that they breed all the year round. The only other statement concerning the breeding is, so far as I know, by Moseley (No. 20). He states that the young are born in July. This is undoubtedly correct, for the live specimens received by me at the end of July gave birth to fully-developed young on the voyage, and directly after reaching England, and those examined contained, in the great majority of cases, either old embryos or none at all.

On the other hand, the specimens which came in December contained, in the great majority of cases, unsegmented and segmenting ova. But in a few (small specimens) the uterus was empty, and again, in a still smaller number, there were old embryos, and in some a few old embryos coexisted with the more numerous young ova. These observations seem to me to show that the eggs pass into the uterus in November and December, and that the young are born in July; in other words, that the period of gestation is eight or nine months. This conclusion is, however, not borne out by Captain Hutton's state-

ment<sup>1</sup> (No. 19), that he has "never opened one which did not contain embryos;" and that he found the uterus full of embryos in September and November. It must be admitted, therefore, that the point cannot be settled on the evidence before us. It is much to be regretted that none of the New Zealand naturalists have taken the trouble to determine a point so easy of observation.

With regard to the sexual relations, I am inclined to think that copulation does not take place, and that the end of the vas deferens, which I have called the ductus ejaculatorius, is not protrusible. I have, indeed, observed in spirit specimens small white ovoid bodies, which closely resemble the spermatophores of the South African species, and I think there can be no doubt that the sexual relations are the same as in those species. The period of the year at which fertilisation is effected is unknown. Hutton has observed that the receptacula contain spermatozoa in November, but are empty in September. This observation distinctly confirms my deduction that the ova pass into the oviduct in November or December.

Before leaving this subject I may mention that I can entirely confirm Hutton's statement that the eggs are often extruded before the development is completed. This may possibly be a reminiscence of the time, probably not very remote, when the eggs were laid in the normal Arthropodan manner—a view which receives support from the thick shell, large size, and heavily yolked nature of the ovum of this species.

### **Peripatus Leuckarti.**

Locality, Queensland.

*Australasian Peripatus, with fifteen pairs of legs, an accessory tooth on the outer blade of the jaw, and a white papilla on the ventral side of the last leg of the male.*

The following observations were made on two specimens most kindly placed at my disposal by Professor Jeffrey Bell, to whom they were sent by Dr. Ramsay, of Sydney. They were found

<sup>1</sup> It should be noted that Hutton does not state whether his observations were spread over the whole year.



(vide No. 44) near Wide Bay in Queensland. The finder's name has not been communicated to me.

Both the specimens were much contracted and the feet bent ventrally on the legs, so that it was difficult to get a good view of the ventral surfaces of the feet.

The length of large specimen	.	.	.	16—17 mm.
„ „ small „	.	.	.	9—10 mm.

The large specimen was a female, and the small a male.

Generally it may be said of these specimens that they resemble almost exactly the New Zealand species. After careful search I have only been able to find three minute points of real difference between them. These are:

1. The outer blades of the jaws have an accessory tooth at the base of the main tooth, as in the Cape species.

2. The male has a rounded white papilla on the ventral face of the fifteenth leg, on each side of the genital opening. It is in the same position with regard to the leg as the corresponding structure in the Cape males.

3. The pigment on the ventral surface is much less conspicuous in this than in the New Zealand species, so that the mottled appearance presented by the ventral surface of the latter species is not found in these specimens. The pigment on the ventral surface of these specimens is much more marked in the lower parts of the papillæ than elsewhere. In the skin between the papillæ and at the apices of the papillæ the pigment is so faint as to be hardly discernable. The result is that to the naked eye the ventral surface appears quite pale with coloured papillæ projecting from it. The predominant pigment of the ventral surface is the blue, but orange is present. The hind end of the ventral surface in the region of the last three legs is darker than elsewhere, in consequence of the great number of the pigmented papillæ.

In addition to the above characters, it may be mentioned that the genital papilla of the female is remarkably prominent, and bears at its free end a longitudinally disposed slit. In the male the genital papilla is fairly prominent, but its aperture is

wider and more rounded, resembling the same structure in both sexes of the New Zealand species. I append a short general description of the two specimens.

There are fifteen pairs of legs. The ventral surface is pale, dotted uniformly with pigmented papillæ, which are more numerous behind. The dorsal surface is dark, and has a median white line. The pigment is of the two colours found in the New Zealand species, viz. bluish to green, and orange to brown. The blue pigment is much the most conspicuous on the dorsal surface. The antennæ are blue mainly, but possess some orange pigment arranged in rings round their basal halves.

The genital papilla, which is remarkably prominent in the female, is between the legs of the fifteenth pair. The feet and legs resemble exactly, so far as could be made out, those of the New Zealand species. The feet have the median dorsal papilla so characteristic of that species; there are three pads on the legs, and a patch of blue pigment round the opening of the nephridia.

If there is any difference, it relates to a faint double row of somewhat turgid papillæ proceeding outwards from the opening of the nephridium along the ventral surface of the leg. The same feature is present in a much more marked form in *P. capensis*. The opening of the nephridium is perhaps slightly more conspicuous than in the New Zealand species. The last leg of the male presents a white papilla on its ventral surface. The outer blade of the jaw has an accessory tooth.

The internal anatomy resembles, so far as I could make out, that of the New Zealand species.

In the female the ovaries were attached along their whole length, and possessed numerous oval white eggs of an average length of .27 mm. In addition there were some larger eggs of a yellowish colour, some of which were attached to the ovary, and some broken away and lying in the body cavity. The largest of these measured .75 mm. in length. They were full of yolk and without any visible membrane.

Each oviduct possessed the receptaculum seminis in a

position similar to that of the same structure in *Peripatus novæ-zealandiæ*. The uterus was empty.

In the male the genital organs were normal, and the unpaired portion of the vas deferens was long, and apparently of a similar structure to that of the New Zealand species.

The specimens were not sufficiently well preserved for an examination for the accessory glands.

### PERIPATUS FROM THE NEOTROPICAL REGION.

*Peripatus* is found all over the northern part of the Neotropical region. It is reported from Chili, Columbia, Cayenne, Venezuela, Nicaragua, and from many of the West Indian Islands, viz. Jamaica, Cuba, Trinidad, St. Thomas. I unfortunately have only been able to make a complete study of the species from Venezuela and of that from Demerara; of some of the remainder I have only seen single specimens, or specimens the preservation of which was not sufficiently good to allow of the determination of specific characters. A partial exception must be made in favour of the small species from Trinidad, of which Dr. J. v. Kennel has been good enough to send me two specimens; but these were, unfortunately, somewhat contracted and not sufficient in number to enable me to generalise as to specific characters. I trust, however, that the careful description of the Venezuela species, the specimens of which were collected by Professor Ernst at Caracas, and given to Professor Balfour, will form a groundwork on which future collectors of *Peripatus* from this region will be able to work.

Although I have failed in determining the relations between the various specimens of *Peripatus* which have been found in the Neotropical region, still I have seen enough to be able to establish a certain number of characters which distinguish a great number—and probably all—of the neotropical *Peripatus* from those found in other regions. Those characters are stated in the following definition :

### General Characters of the Neotropical Species.

With four spinous pads on the legs, and two papillæ on the anterior side of the foot. With generative aperture between the legs of the penultimate pair. Dorsal white line absent, and papillæ arranged in a single row on the ridges of the skin. Many of the primary papillæ have a terminal portion slightly constricted off from the main portion. Outer blade of jaw with one minor tooth, inner blade with one minor tooth next the main tooth (fig. 25), and a row of smaller minor teeth separated from the latter by a diastema. Unpaired part of vas deferens of great length. Ovary with oviducts entering its anterior end, and attached to pericardial floor by a single band of great length from the opposite end. Each oviduct provided with a receptaculum seminis with double duct, and with a thin-walled receptaculum ovorum. Ova minute without yolk. Embryos of very different ages in same uterus, and births probably taking place all the year round. Males generally smaller than females, and frequently with a smaller number of legs. The number of legs often inconstant in the same species in the same sex; in fact it may be said that the number of legs varies in all the Neotropical species which are at all well known. The opening of the nephridium of the fourth and fifth legs is on a papilla which is quite separate from the third pad (fig. 11).

### *Peripatus Edwardsii.*

*Neotropical Peripatus from Caracas with a variable number of legs—the smallest number being twenty-nine and the greatest thirty-four. Males with twenty-nine and thirty legs, and tubercles on a varying number of the posterior legs. The basal part of primary papillæ are cylindrical.*

I propose to reserve the name *Edwardsii* for the Neotropical species, which is best known, viz. that from Caracas. This has been described by Ernst and Gaffron. Whether the specimens obtained by Audouin and Milne-Edwards from Cayenne and named *Edwardsii* by Blanchard (No. 8) belong to



this species cannot be definitely settled until more specimens come to hand.

In **P. Edwardsii** the females are larger than the males and have a greater number of legs. This fact was first noticed by Gaffron. He found that the males possessed either twenty-nine or thirty legs, while of his females one had thirty-four, four had thirty-two, and four thirty-one. In my specimens, which came, I believe, from the same place as the specimens which Gaffron used for his<sup>1</sup> second paper (No. 35), all the males had thirty or twenty-nine legs (four with thirty and three with twenty-nine), while of the females three had thirty-one, four had thirty-two, and one twenty-three (fig. 6). Ernst states that the full-grown animal has thirty-one pairs of legs, the new-born young but twenty-nine; and he deduces from this that the young are born with an incomplete complement of legs, and that new legs make their appearance in the subsequent growth of the animal. This, if true, would be important, as in no species of *Peripatus* that I know of are the young born imperfect in this respect. I therefore examined the number of legs of the oldest embryos in my specimens with great care, and the result of my observations is in entire contradiction to Ernst's statements. The embryos I found differ in the number of legs, just as do the adults, the greatest number being thirty-two pairs and the smallest twenty-nine. If this is so there can be no doubt that the new-born young differ in the same manner. To take an instance: from the lower end of the uterus of the four specimens with thirty-two legs I obtained in all seven embryos, which were practically fully-developed and ready for birth. Of these, four had twenty-nine legs, two had thirty-one, and one had thirty-two—an embryo with twenty-nine and one with thirty legs were found in the same mother; and I have also found instances of a quite immature embryo (but possessed of the full number of legs) with a greater number of legs than the large mature embryo which occupied the part of the uterus

<sup>1</sup> The specimen which Gaffron used for his first paper was from Trinidad, and had thirty-two legs.

next the external opening. Considering the easy nature of the observations required, Professor Ernst's statements display a very extraordinary method of work.

**Colour.**—My observations on this point were made on spirit specimens, and cannot therefore have the value of those of Ernst, who had the living animals before him. He says: "The colour is brownish black, with a diffused black line on the middle of the back; the ventral side is dark flesh-coloured."

In all my preserved specimens the colour was brown, darker in some than in others; in the specimen figured it is as dark as in any in my possession. The ventral surface, moreover, was of the same colour as the dorsal. As these specimens came from Caracas, and have become distinctly paler since I first saw them, it seems pretty clear that the colour of this species is much affected by spirit. It will be remembered the brown pigment of *P. capensis* was changed by the action of spirit. The same fact has been observed by Grube (see below, p. 480), who found that the pigment was partly dissolved by the spirit, and also by myself in some specimens brought alive from Demerara by Mr. W. L. Sclater (No. 41).

**The Ridges and Papillæ of the Skin.**—The ridges are more clearly marked, and the papillæ of the dorsal surface are less numerous. The dorsal white line is not present, so that the ridges are continuous right across the dorsal middle line. Further, there is for the most part only one row of papillæ on each ridge, whereas in the South African and New Zealand species there is considerable irregularity in this respect. The fine diagonal lines, which break up the rows of papillæ into lozenge-shaped areas, are absent in this species. The ridges extend for the most part right across the dorsal surface, but here and there, particularly at the level of the legs, there are accessory ridges extending across the middle line and stopping short a little distance on each side of it. They cause a slight deflection of the contiguous main ridges (fig. 6). Many of the papillæ—particularly those on the legs—are divided by a constriction into two main portions (fig. 12)—

a free portion bearing the spine and a larger basal part. The basal part is cylindrical, and the terminal portion often of considerable size. Those immediately round the lips appear to be without this characteristic.

**The antennæ** present no features of specific interest. The tongue and lips are without pigment and have the typical form.

**The jaws** present differential characters. The outer blade (fig. 26) has a well-marked minor tooth in addition to the main one. On the inner blade the number of minor teeth varies (generally eight), and the anterior of them is close to the main tooth and larger than the rest, which are separated from it by a diastema (fig. 25).

**The oral papillæ** are normal.

A typical **ambulatory appendage** presents the following characters (fig. 12). The leg possesses four spinous pads, a strongly marked, rather deep groove in the position of the tumid papillæ of *Capensis*, i.e. a groove placed on the ventral surface of the leg, and extends from the opening of the nephridium as far as the third or fourth row of papillæ from the proximal pad. This groove may be widely open as in the leg figured, or its edges may be approximated so that it appears as a slit. The papillæ at its margin are somewhat larger and more indistinct than the ordinary papillæ. The foot resembles that of *Capensis* in possessing two papillæ on its anterior face, but the two basal papillæ are absent.

The opening of the segmental organ of the fourth and fifth legs is on a papilla which is placed on the proximal side of, and quite separate from, the third pad, between it and the proximal pad (fig. 11). This feature is found in all the neotropical species which I have examined. On certain of the posterior legs of the males there are two and sometimes one smooth white tubercle with an opening at their extremities (fig. 22). They are placed close behind the groove, and are found only on the posterior legs. Their exact arrangement varies in different individuals. To give examples :

In a male with 30 legs :

*Right side.*—Legs 21—24 inclusive, each had one such tubercle ; legs 25—28 inclusive, each had two such tubercles ; legs 29 and 30 were without them.

*Left side.*—Leg 21 had one tubercle ; leg 22 was without one ; legs 23 and 24 each had one ; legs 25—28 inclusive, each had two ; legs 29 and 30 were without them.

In another male with 30 legs :

*Right side.*—Leg 23 had one tubercle ; legs 24—28 inclusive, each had two ; legs 29 and 30 were without.

*Left side.*—Leg 22 had one ; legs 23—28 inclusive, each had two ; legs 29 and 30 were without them.

When one papilla only is present it is the distal one.

From these examples it is obvious that the arrangement of these tubercles is different not only in the different individuals but also on opposite sides of the same individual. The last two legs are always without them. Gaffron found precisely the same irregularity in the arrangement, but in his specimens they were symmetrical. In one with thirty legs, the twenty-second leg had one, and legs 23 to 28 each had two tubercles. While in another male with twenty-nine legs, leg 20 had only one, while legs 21 to 27 each had two. The pits at the apices of these tubercles are, according to Gaffron, the openings of glands corresponding to the crural glands of *Capensis*.

The legs of the last pair are smaller than the penultimate, and possess only two spinous pads. The legs of the penultimate pair are without the nephridial opening, and the pedal groove is inconspicuous as it is in the last pair. I could not satisfy myself whether the legs of the last pair possessed a nephridial opening ; but Gaffron states that they possess a nephridium.

Gaffron (No. 35) describes a peculiar bean-shaped papilla, placed in a pit of the integument on the dorsal surface of the leg near the foot. Its surface is smooth as is also the lining of the pit in which it is placed. It is found in the Trinidad species, and may very probably turn out to be characteristic of the neotropical species.



**Internal Anatomy.**—Excepting the generative organs there is nothing in the internal anatomy of this species which deserves notice here. The generative organs, of which we have an excellent description by Gaffron, do, however, present some features of interest. The generative opening in both sexes is between the legs of the penultimate pair. The oviduct end of the ovary is directed forwards, and the ovarian ligament, which is attached to the opposite end of the ovary, is of great length, being attached to the pericardial floor between the twenty-fifth and twenty-sixth pairs of legs. A globular receptaculum seminis (with two short ducts) opens into the anterior part of each oviduct. Immediately in front of the receptacula each oviduct gives off a short diverticulum, called “cæcum” by Ernst, “zipfelformige Anhang,” and “ovarial-trichter” by Gaffron. Gaffron, who at first thought that this process opened at its free end into the body cavity, now accepts Kennel’s statement that it opens into a small vesicle with extremely thin walls. Kennel calls this vesicle the receptaculum ovarum. I have seen the process, but, unfortunately, have no observations on its termination; but I am strongly inclined, on theoretical grounds, to think that Kennel is correct in his statement as to the delicate vesicle. The generative ducts are the modified nephridia of the segment on which the external opening is placed: this is proved, on the one hand by their development, and on the other by the fact that nephridia are absent from the penultimate legs, between which the generative opening is placed. Now, it has been shown by me (No. 39) that all the nephridia open internally, not into the body cavity as has been supposed, but into a small vesicle with extremely delicate and thin walls. It thus appears that the presence of this delicate vesicle of the receptaculum ovarum is another proof—if another were wanted—that the oviducts of *Peripatus* are modified nephridia. No such structure has been found in the New Zealand species, but, possibly, further investigations may come upon it. In *Capensis*, for reasons which I have set forth elsewhere (No. 39, Part 3), one would not expect to find this structure.

The male organs differ from those of the Cape species and resemble those of the New Zealand species in the fact that the common posterior part of the testicular ducts is of great length. A very good description of it has been given by Gaffron. A pair of accessory glands is present in the male. They open on each side of the anus (Gaffron).

Nephridia are present in the legs of the last pair but are absent from the penultimate legs, between which the generative opening is placed (Gaffron, No. 35). With regard to the **crural glands**, Gaffron states that they are absent from the female, and only present in the males in those legs provided with the tubercles described above.

The ova are small and without yolk. Their development has been described in a closely-allied species from Trinidad by Kennel, according to whom the embryos acquire a placental connection to the uterine wall and an amnion. These structures are, however, said to disappear after a certain stage is reached, and there is reason to doubt whether they have the relations, significance, and method of development which Kennel ascribes to them (Selater, No. 46).

The uterus contains embryos in all stages of development, and the young, which are fully developed at birth, are presumably born at different times of the year.

The length of mature embryos of *Peripatus Edwardsii*, lying stretched out in the uterus with head near generative opening, is about 20 mm.

The length of a large adult female is 55 to 60 mm. The males, of course, are rather smaller.

**Habits.**—The habits of this species are apparently much the same as in the other species. A large number of specimens were found by Ernst in a yard of the University building of Caracas under heaps of rubbish.

Peters (No. 24) mentions specimens from the following localities in Venezuela:—Caracas, Puerto Cabello, Laguayra. He states that some of the specimens from Puerto Cabello have thirty and others thirty-two pairs of legs.

### **Peripatus from Demerara.**

In January of this year (1887) Mr. W. L. Sclater brought to England twenty female specimens of *Peripatus* collected at Maccasseema, on the Pomeroon River. The specimens, when they came into my hands, were torpid and apparently at the point of death, and it was necessary to open them at once and remove the embryos. I was unable therefore to make a detailed examination of them in the fresh state.

Mr. Sclater has already (No. 41) given a short description of the specimens. To his description I add here notes of my own observations, made on the first arrival of the animals, and an account of those which I have since made on their preserved bodies.

All the specimens (twenty in number) were females. The colour was a dark brown on the dorsal surface, with a median diffuse dark stripe, such as Ernst describes. The antennæ were of a darker colour than the rest of the body. The ventral surface was higher than the dorsal—a kind of flesh colour. The animals turned quite red in spirit, and the red colouring matter was gradually dissolved by the spirit leaving them a lighter brown.

In well-grown specimens the uterus contained ten embryos in each horn, of which the fifth from the ovary was generally in the spiral stage. The receptacula ovarum seemed to contain ova, which were 0.38 mm. in diameter. The large eggs in the ovary were the same size.

In one specimen, which I carefully examined for the purpose, there were cilia in the receptacula seminis in the position described by Gaffron. There can be no doubt of their presence. I saw them in active movement. I am very glad to have had the chance of confirming Gaffron on this point. The older embryos had the same colour as the adult. I could not be certain of the presence of spermatozoa in either the receptaculum seminis or in the oviduct. If present at all, they must have been few in number.

To these observations I have now the following to add: The colour, under the prolonged action of spirit, has become lighter. The antennæ, oral papillæ, jaws and legs, resemble in all respects the same structures in the Caracas specimens. The grooves on the legs were for the most part closed and therefore slit-like. None of them possessed tubercles.

Mr. Sc Slater has the following statement on the slits and tubercles. "In my specimens and in that from Dominica, the openings (i. e. the slits) are in many cases rounded, and sometimes have attached to them a bladder-shaped appendage." I do not quite understand this passage, but if it means that the slits are round openings and that there are tubercles in the specimens he brought from Demerara, I cannot confirm his statement. It is unfortunate that no males are to hand, as it is important from a systematic point of view to know if they have the tubercles such as are found in the Caracas species, and if they differ from the females in the number of legs. The length of a large specimen was 55 to 60 mm.

Mr. Sc Slater states that all the specimens examined by him, including those taken from the uterus, had thirty pairs of legs. Mr. Sc Slater's observations must have been confined to a very small number of his specimens. I examined fourteen adults: of these seven had thirty pairs of ambulatory legs, six had thirty-one, and one had twenty-seven. Out of thirteen embryos examined seven have thirty pairs and six have thirty-one. Unfortunately, I did not notice that the adults varied in the number of their legs, until after the embryos had been removed from all except the specimens with twenty-seven pairs of legs; so that it was not possible to determine, excepting in this case, whether the young resembled their parents in this respect. Out of four embryos which had already developed the full complement of legs and were removed from the specimen with twenty-seven pairs, three had twenty-seven and one had twenty-eight pairs of ambulatory legs, so that it appears that the number of legs varies in the species.

The only other difference between these specimens and those from Caracas that I could detect, related to the primary



papillæ on the skin. In the Caracas species, as already mentioned, these have comparatively narrow cylindrical bases, and the diameter of the tops is often almost as great as that of the basal portion. In the Demeraran specimens, on the other hand, the lower portion of the papillæ have the form of truncated cones with very broad bases, while the tops are relatively, and I think absolutely, much slenderer than in the Caracas specimens. The papillæ figured by Gaffron (No. 34, Pl. VII, and here reproduced fig. 27) resemble those of the Demerara specimens, and will serve for comparison with the papillæ of the Caracas specimens shown on Pl. XXXVIII, fig. 12. I propose provisionally to regard these specimens as belonging to a distinct species, and to call it **P. demeraranus**<sup>1</sup> with the following characters. *Neotropical Peripatus with twenty-seven to thirty-one pairs of ambulatory legs and cylindrical primary papillæ. Locality Maccasseema, Demerara.*

### Peripatus from Trinidad.

Dr. J. v. Kennel (No. 31) found two distinct species of *Peripatus* in Trinidad; one of these he calls *P. Edwardsii* and the other *P. torquatus*. His description of both is unfortunately extremely meagre.

The species which he calls *Edwardsii* possesses twenty-eight to thirty pairs of legs (No. 32). The generative opening is between the legs of the penultimate pair, and the generative organs present the characters of the Neotropical species.

Dr. Kennel was kind enough to send me two of this species in spirit, and I am able to supplement his description.

<sup>1</sup> Slater (No. 46) gives the name *im Thurni* to the specimens with thirty pairs of legs, which he has observed. It is of course quite possible that the specimens with thirty pairs may be specifically distinct from those with twenty-seven and thirty-one pairs. This, however, as stated above, I do not regard as probable. On account of this uncertainty, and also because of the further uncertainty as to whether the Demeraran specimens are specifically distinct from species already determined and named, I propose the provisional name of *Demeraranus* to include all specimens from Demerara, whether the number of legs be twenty-seven, thirty, or thirty-one pairs.

One of these specimens had thirty-one pairs of legs and the other thirty, from which it appears that Kennel, like so many other zoologists who have examined *Peripatus*, has not been very careful in counting the legs. The dorsal surface was of a chocolate colour, the ventral surface being a light brown. The papillæ and ridges of the skin presented the features characteristic of the Neotropical species. The bases of the primary papillæ are conical as in *Demeraranus*. The jaws also presented no points of difference from those of the species from Caracas, excepting that possibly the number of minor teeth was rather larger: in one I found as many as eleven.

I think there can be no doubt that this is a distinct species, and I propose to call it and define it as follows:

***Peripatus Trinidadensis* (*Edwardsii*, Kennel).**

*Peripatus from Trinidad, with twenty-eight to thirty-one pairs of ambulatory legs, and a large number of minor teeth on the inner blade of the jaw. The basal portions of the primary papillæ are conical.*

***Peripatus torquatus* (Kennel).**

*Peripatus from Trinidad of large size, with forty-one to forty-two pairs of ambulatory legs. The head is marked off from the body by a bright yellow band on the dorsal surface.*

The larger species is named *P. torquatus*, and Kennel gives the following description of it. "The females reach the length of 15 cm., with a diameter of 8 mm., while the males have a length of about 10 cm. The colour of the dorsal surface is red brown, the middle line of the back being somewhat darker, and paling off towards the sides. The head with the tentacles is black and is marked off from the body on the dorsal side by a bright yellow band, which often shows a small interruption in the middle line. The ventral surface has a dark flesh colour. There are forty-one or forty-two pairs of legs.

This completes the list of the Neotropical *Peripatus* of which we have anything like detailed knowledge. The remain-

der of this monograph will be devoted to a statement of all that is known with regard to the specimens found in other localities.

1. The original species found by Guilding (No. 1) in the forests of the Island of St. Vincent in the Antilles, and called by him *P. juliformis*, possessed thirty-three pairs of legs, and a dark line down the centre of the back. The generative opening is apparently immediately in front of the penultimate legs. The animal was of a fair size, being three inches in length by three lines in breadth. It is apparently similar in all essential respects to other neotropical *Peripatus*, and I am inclined to maintain for the present the species, and to define it as follows :

### ***Peripatus juliformis* (Guilding).**

*Neotropical Peripatus from St. Vincent, with thirty-three pairs of ambulatory legs.*—This definition is exceedingly unsatisfactory because it is based on the number of legs, which, as I have stated, varies in all the species which have been closely examined.

2. The species described by Audouin and Milne-Edwards (No. 2) possessed thirty pairs of ambulatory legs, and came from Cayenne (on the banks of the River Approuague, three leagues from its mouth). The specimens were found “unter faulem, im Schlamme versunkenem Holze, an den Ufern des Approuage im Brackwasser.”

The description is very imperfect, as may be judged from the fact that the generative aperture is not even mentioned.

The species was regarded by the authors as identical with Guilding's *P. juliformis*, but subsequently Blanchard (No. 8) gave it the name of *P. Edwardsii*. I propose to retain the latter name and to regard it as belonging to the same species which I have fully described above from Caracas.

It must, however, be remembered that the characters of *P. Edwardsii*, as given in this monograph (p. 467) are based on the Caracas specimens; and it may quite well happen that the

*Peripatus* found at Cayenne, when better known, will turn out to be a distinct species.

3. Wiegmann (No. 4) obtained a specimen of *Peripatus* from near the Valentia Lake in Columbia, with thirty pairs of legs. It is quite impossible to say whether this is a distinct species or not. It possesses, according to Wiegmann's description, four spinous pads on its legs and a generative opening between the legs of the penultimate pair.

4. C. Mority (No. 5) obtained a large number of *Peripatus* from the Island of St. Thomas. He gives no details.

There is a specimen in the British Museum from St. Thomas. It has twenty-eight pairs of ambulatory legs, and is of a yellowish-brown colour, but is unfortunately too ill-preserved for determining any specific characters.

5. Peters (No. 24) mentions specimens from Utuado, Porto Rico, and gives the following particulars.

Specimens	21 mm. in length	had	27	pairs of legs.
„	33 mm.	„	30	„
„	38 mm.	„	31	„
„	42—48 mm.	„	32	„

6. Blanchard (No. 8) has described a *Peripatus* found in Chili by M. Claude Gay, with nineteen pairs of legs. His description is as follows:—"Le corps est long de 30 à 32 mill., et large de 5 à 6, légèrement atténué aux deux extrémités, mais surtout vers la partie postérieure. Sa couleur est noire, un peu variée irrégulièrement de taches roussâtres. La tête est presque carrée avec les antennes amincies vers le bout, présentant des annulations très serrées. L'orifice buccal est ovale. Les pattes sont au nombre de dix-neuf paires, ciliées de poils raides comme de petites pointes, et terminées par des crochets."

There is obviously nothing in this description which enables us to say whether the three specimens at the author's disposal possessed the characters of the Neotropical species or not. It is extremely probable, considering the remoteness of the locality, that this is a distinct species; but unfortunately



Blanchard has not, with the exception of a name, assigned to it any feature which can be in the least degree regarded as specifically distinctive. He calls it *P. Blainvillei*, and says that it has nineteen pairs of legs. The name I propose to discard, and the statement of fact I am inclined to doubt, for this reason:—In Gay's 'Historia de Chile,' vol. iii, "Zoologia," p. 58, there is a description of this proposed new species, and the possession of nineteen pairs of legs is given as a character. I presume Blanchard is responsible for this statement as it coincides with that given in No. 8. In the description reference is made to some figures in the Atlas. These turn out to be a dorsal, ventral, and side view, &c., of the specimen described. Will it be believed that not only does each of these figures show a different number of legs, but in the case of the dorsal and ventral views, the numbers on the right and left sides are different? The details are as follows:

Dorsal view, right side,	27	legs and oral papilla.
"    "    left    "	26	"    "
Ventral "    right    "	33	"    "
"    "    left    "	31	"    "
Side view of left side,	20	"    "

I do not know who is responsible for these figures. The draftsman's name on the plate is Spinola. I need hardly say that, if they are a fair sample of the drawings in the Atlas, the zoological plates are not worth the paper they are printed on.

It will, perhaps, be convenient to denote the fact that there is a *Peripatus* in Chili, by introducing for it the provisional name of ***Peripatus chiliensis***.

7. Blanchard refers to a *Peripatus* found in Cuba by M. Macleay. He regards it as belonging to the species *juliformis*. I have been unable to find any account of this Cuban species.

8. Grube (No. 11) describes three specimens of *Peripatus* from near Colonia Towar, in Venezuela, and referred them to *P. Edwardsii*. One of the specimens possessed twenty-nine pairs of legs and the other two thirty each. But one cannot regard his statements on this head as being trustworthy, in-

asmuch as the specimen he has figured has thirty-one pairs (in addition to the oral papillæ).

He found a number of embryos in the uteruses of his specimens, all of which, excepting one with thirty, possessed thirty-one pairs of legs.

His statement on the colour is interesting, as tending to show that the pigment in this species is affected by the prolonged action of spirit. He says :

“Die Färbung war an einem sehr frisch erhaltenen Weingeist exemplar ein dunkles unreines Kirschroth, der Weingeist, indem es lag, hatte sich blassroth gefärbt, bei denen die längere Zeit aufbewahrt waren, ging der Ton in's Braunlichgrue über, doch blieb die Rückenseite immer sehr viel dunkler als die Bauchseite, auch zeigte sie beständig die schon von den früheren Beschreibern erwähnte mittlere Längsfurche von noch dunklerer Farbe, rechts und links von ihr in einiger Entfernung sieht man gewöhnlich noch eine dunkle Seitenlinie.”

I cannot be quite certain from Grube's figures whether the papillæ have the form characteristic of the Caracas species or of the *Demerara* form.

The species possesses all the Neotropical characters, viz. inner blade of jaw with minor teeth separated by diastema from the first small tooth, legs with four spinous pads, generative opening between the penultimate pair of legs, oviducts with receptaculum and process, embryos in uterus of very various ages.

I propose, therefore, to retain provisionally Grube's name for the specimens from Colonia Towar, and to regard them as belonging to the species found at Caracas, and described above as *P. Edwardsii*.

9. Mr. Thomas Belt found a specimen of *Peripatus* at Santo Domingo, in Nicaragua. The specimen (dried) is referred to in his work, 'The Naturalist in Nicaragua' (p. 140), and has been examined by Professor Moseley, who found that it possessed thirty-one pairs of ambulatory legs.

**P. quitensis** (Schmarda).

10. Professor Jeffrey Bell has recently (No. 43) drawn attention to a reference by Schmarda in his 'Zoology' (No. 42) to a species with thirty-six pairs of legs from Quito, in Ecuador. Schmarda gives a figure of the specimen, which came from an elevation of 9000 feet.

**Neotropical Peripatus in the British Museum.**

1. Specimen from Dominica found by Mr. G. F. Angas. This specimen is in excellent condition, and has twenty-nine pairs of ambulatory legs. It has been shortly described by Professor Jeffrey Bell (No. 29), who says that it has thirty pairs of legs. This may be so, but I could not make out more than twenty-nine. The dorsal surface is brown, and there is a dark streak (chocolate-coloured with a dash of purple) running along the sides of the body just dorsal to the legs. The legs are without tubercles. The pedal grooves are widely open. The papillæ are, I think, conical in form; but the light was not good enough to enable me to obtain certainty on this point.

2. A specimen marked *P. Blainvillei*, without locality. This has thirty-three pairs of ambulatory legs, and is of a reddish-brown colour. It is very much contracted. There were no tubercles, and I was not able to make out the shape of the papillæ.

3. A specimen marked *P. Blainvillei*, without locality (see above, p. 479), with twenty-eight pairs of ambulatory legs.

4. There are three specimens in a bottle labelled "From Jamaica," collected by Gosse.

They are all a yellowish brown. Two of them have thirty-one and one thirty-seven pairs of ambulatory legs. The latter is remarkable as being the smallest of the three, measuring in the contracted condition 22 mm. Of the two with thirty-one pairs of legs, the largest measured about 48 mm., and the other about 22 mm. The papillæ were conical and there were no tubercles. Mr. Gosse, in 'A Naturalist's Sojourn in Jamaica' (P. H. Gosse, London, Longmans, 1851,

p. 62), refers to these *Peripatus* in the following terms: "*Peripatus* found at Bluefields mountain above Bluefields House, near the town of Savanna lo Mar. The mountain height is four or five miles from Bluefields. Here, around a piece of burnt ground just reclaimed from the forest, but not yet planted, were found, under stones, five or six specimens of *Peripatus*, one twice as large as any of the others. The piece of ground lay at the foot of a conical peak of considerable elevation, but not the very loftiest, covered with original forest. It is a curious creature, and I think rather allied to the Annelida than the Mollusca. It is of a velvety appearance, of a blackish-brown hue, the tentacles tipped with white. From these latter organs there exudes, when the animal is touched, a thick glutinous substance, as adherent as birdlime." He concludes that it is of a different species from that found by the Rev. L. Guilding at St. Vincent.

5. A specimen labelled "*Peripatus juliformis*, West Indies, Mr. Gibson, *Nereis viridis*, Adams, 'Linn. Trans.,' feet only thirty-one pairs."

This specimen was about 65 mm. in length,  $5\frac{1}{2}$  in breadth, 5 in dorso-ventral depth; i. e. it was cylindrical in form. It possessed thirty-two pairs of ambulatory legs, and has a very pale brown colour (almost white). Its skin is much smoother than is generally the case.

The legs have four spinous pads, and are without tubercles; the generative opening is between the legs of the penultimate pair; the integumentary papillæ are constricted; the legs of the last two pairs are very small. It clearly, therefore, belongs to a typical Neotropical species, but more than this cannot be said.

6. A smaller specimen with thirty pairs of ambulatory legs of very much the same colour and form. It was labelled, "*Peripatus juliformis*, Guild., W. Indies? Sloane collection."

It possesses thirty pairs of legs. The generative opening is between the legs of the penultimate pair. The grooves on the base of the legs fairly well marked. Feet not sufficiently well preserved for study (claws broken away). The integu-



mentary papillæ constricted, and arranged on the dorsal surface in regular rows. Length about 48 mm.; body cylindrical in shape with a diameter of about 4 mm. The legs are without tubercles.

7. Finally there is a specimen labelled "*Peripatus Santarem*, Wickham, purchased of W. H. J. Carter." It has thirty-one pairs of ambulatory legs, and presents, so far as its external features are concerned, the Neotropical characters. The papillæ are conical, and the legs are without tubercles.

Professor Strunstrip was kind enough to send me for examination the specimens in his museum. I desire to take this opportunity of thanking him for his courtesy and kindness in the matter. The Copenhagen specimens were in four bottles:

(1) Label "*Peripatus Edwardsii*, Bl., Vestindien, Krøyer." This was a fine, well-preserved specimen, with thirty-one pairs of ambulatory legs, and a brown colour. The dorsal surface was darker than the ventral. The dorsal papillæ were remarkably large (fig. 14) and constricted, as were also the ventral, but less markedly. The generative opening was between the legs of the penultimate pair, and the spinous pads of the legs were four in number.

(2) Label "*Peripatus Edwardsii*, Blanch., St. Croix, Krøyer." This specimen, which in general appearance resembled the first, but was smaller, possessed twenty-seven pairs of ambulatory legs. Spinous pads and generative opening as in (1).

(3) Label "*Peripatus Vestindien*, Hombek (?)." With thirty-two pairs of ambulatory legs.

(4) The specimen in the fourth bottle was not sufficiently well preserved for observation.

It is unfortunate that the exact localities of the above were not recorded. They are obviously all Neotropical species, but to which of these they belong cannot be at present settled.

Four specimens of *Peripatus*, of which one had thirty-one pairs of legs, are reported from Demerara (Hoorubea Creek, twenty miles from Georgetown, on east side of Demerara river), by Mr. J. J. Quelch (No. 36). No details are given.

A single specimen was found at Breves, on the Island of Marajo, at the mouth of the Amazon, by Mr. J. C. Branner (No. 37). No details are given.

#### PERIPATUS SUMATRANUS.

A single specimen of *Peripatus*, stated to have come from Sumatra, has recently been described by Dr. R. Horst (No. 38). The evidence that the specimen was actually found in Sumatra is not, however, conclusive. Dr. Horst states that it was found in a bottle containing insects from East Sumatra. The name of the finder is not given, and there is no evidence to show how the specimen got into the bottle. Considering the fact that this is the only specimen of *Peripatus* ever reported from the Oriental region, it will be prudent to suspend our judgment as to the authenticity of the locality given by Dr. Horst. The specimen has twenty-four pairs of ambulatory legs, and is 25 mm. in length. The papillæ are constructed as in the Neotropical species, and are apparently on the cylindrical type. Dr. Horst describes them as "appearing to consist of a truncated cone, bearing on its top a small cylinder provided with a spine." The legs have four pads, the generative opening is between the legs of the penultimate pair. All these are Neotropical characters. The anus is not quite terminal. Colour is dark blackish brown; the ventral surface is paler, greyish. "Some small white spots scattered on the dorsal surface, but they seem only to be produced by the loosening of the cuticle from the top of the papillæ." The foot carries only two papillæ, one on the anterior and one on the posterior face. This is unique so far as my experience of *Peripatus* goes. The pedal groove is absent from the two posterior legs as in *P. Edwardsii*. The antennæ have forty-seven rings.

I think that there can be no doubt that this is a distinct species. It is the only specimen hitherto recorded from the oriental region, and it seems a fact of extreme interest that it should resemble the Neotropical species more than any other. It is a great misfortune that Dr. Horst was not able to examine the jaws and generative organs.

### **Peripatus sumatranus** (Horst).

*Peripatus* from Sumatra, with twenty-four pairs of ambulatory legs, four pads on the legs, and constricted papillæ. The generative opening is between the legs of the penultimate pair. The feet have only two papillæ.

## SYNOPSIS OF THE SPECIES OF PERIPATUS.

### **South African Species.**

*With three spinous pads on the legs and two primary papillæ on the anterior side of the foot, and one accessory tooth on the outer blade of the jaw; with a white papilla on the ventral surface of the last fully developed leg of the male. Genital opening subterminal, behind the last pair of fully-developed legs. The terminal unpaired portion of vas deferens short. (Ova of considerable size, but with only a small quantity of food-yolk.*

**P. capensis** (Grube).—*South African Peripatus, with seventeen pairs of claw-bearing ambulatory legs. Locality, Table Mountain.*

**P. Balfouri** (Sedgwick).—*South African Peripatus, with eighteen pairs of claw-bearing ambulatory legs, of which the last pair is rudimentary. With white papillæ on the dorsal surface. Locality, Table Mountain.*

**P. brevis** (De Blainville).—*South African Peripatus, with fourteen pairs of ambulatory legs. Locality, Table Mountain. (I have not seen this species. Presumably it has the South African characters.)*

**P. Moseleyi** (Wood Mason).—*South African Peripatus, with twenty-one and twenty-two pairs of claw-bearing ambulatory legs. Locality, near Williams-town, Cape Colony.*

### **DOUBTFUL SPECIES.**

(1) *South African Peripatus, with twenty pairs of claw-bearing ambulatory legs* (Sedgwick). *Locality, Table Mountain. (Also Peters, locality not stated.)*

(2) *South African Peripatus, with nineteen pairs of ambulatory legs* (Trimen). *Locality, Plettenberg Bay, Cape Colony. (Also Peters, locality not stated.)*

### **Australasian Species.**

*With fifteen pairs of claw-bearing ambulatory legs, with three spinous pads on the legs, and a primary papilla projecting from the median dorsal portion of the feet. Genital opening between the legs of the last pair. Receptacula*

*seminis present. Unpaired portion of vas deferens long and complicated. Ova large and heavily charged with yolk.*

- P. Novæ-zealandiæ** (Hutton).—*Australasian Peripatus, without an accessory tooth on the outer blade of the jaw, and without a white papilla on the base of the last leg of the male. New Zealand.*
- P. Leuckarti** (Saenger).—*Australasian Peripatus, with an accessory tooth on the outer blade of the jaw, and a white papilla on the base of the last leg of the male. Queensland.*

### Neotropical Species.

*With four spinous pads on the legs, and the generative aperture between the legs of the penultimate pair. Dorsal white line absent. Primary papillæ divided into two portions. Inner blade of jaw with gap between the first minor tooth and the rest. Oviducts provided with receptacula ovarum and seminis. Unpaired part of vas deferens very long and complicated. Ova minute, without food-yolk. (Legs not constant in number in the same species.)*

- P. Edwardsii**.<sup>1</sup>—*Neotropical Peripatus from Caracas, with a variable number of ambulatory legs (twenty-nine to thirty-four). Males with twenty-nine or thirty legs, and tubercles on a varying number of the posterior legs. The basal part of the primary papilla is cylindrical.*
- P. Trinidadensis** (n. sp.).—*Neotropical Peripatus from Trinidad, with twenty-eight to thirty-one pairs of ambulatory legs, and a large number of teeth on the inner blade of the jaw. The basal portion of the primary papillæ is conical.*
- P. torquatus** (Kennel).—*Neotropical Peripatus from Trinidad, with forty-one to forty-two pairs of ambulatory legs. With a transversely placed bright yellow band on the dorsal surface behind the head.*

### DOUBTFUL SPECIES.

The above are probably distinct species. Of the remainder we do not know enough to say whether they are distinct species or not. The following is a list of these doubtful species, with localities and principal characters.

- P. juliformis** (Guilding).—*Neotropical Peripatus from St. Vincent, with thirty-three pairs of ambulatory legs.*
- P. Chiliensis** (Gay).—*Neotropical Peripatus from Chili, with nineteen pairs of ambulatory legs.*
- P. demeraranus** (Selater).<sup>1</sup>—*Neotropical Peripatus from Macassar, Java.*

<sup>1</sup> This name was first applied by Blanchard (No. 8) to a species from Cayenne (vide above, p. 478). The description, however, is very imperfect, and it is by no means clear that the Cayenne species is identical with the species here named *Edwardsii*.



*Demerara, with twenty-seven to thirty-one pairs of ambulatory legs and cylindrical primary papillæ.*

*Peripatus* from Cayenne (Audouin and Milne-Edwards).—*With thirty pairs of legs.* Named *P. Edwardsii* by Blanchard. Doubtful species.

*Peripatus* from Valentia Lake, Columbia (Wiegmann).—*With thirty pairs of legs.* Doubtful species.

*Peripatus* from St. Thomas (Moritz).—No description. Doubtful species.

*Peripatus* from Colonia Towar, Venezuela (Grube).—*With twenty-nine to thirty-one pairs of ambulatory legs.* Named *P. Edwardsii* by Grube. Doubtful species.

*Peripatus* from Santo Domingo, Nicaragua (Belt).—*With thirty-one pairs of ambulatory legs.* Doubtful species.

*Peripatus* from Dominica (Angas).—*Neotropical Peripatus, with twenty-nine pairs of ambulatory legs.* Doubtful species.

*Peripatus* from Jamaica (Gosse).—*With thirty-one and thirty-seven pairs of ambulatory legs.* Species doubtful.

*Peripatus* from Santarem.—*Neotropical Peripatus, with thirty-one pairs of ambulatory legs.*

*Peripatus* from Cuba.—No details.

*Peripatus* from Hoorubea Creek, Demerara (Quelch).—*With thirty pairs of legs.*

*Peripatus* from Marajo (Branner).—No details.

*Peripatus* from Utuado, Porto Rico (Peters).—*With twenty-seven, thirty, thirty-one, and thirty-two pairs of legs.*

*Peripatus* from Surinam (Peters).—No details.

*Peripatus* from Puerto Cabello, Venezuela (Peters).—*With thirty and thirty-two pairs of legs.*

*Peripatus* from Laguayra, Venezuela (Peters).—No details.

*Peripatus Quitensis* (Schmarda).—*From Quito, with thirty-six pairs of legs.*

### **Peripatus from Sumatra.**

*P. Sumatranus* (Horst).—*Peripatus from Sumatra, with twenty-four pairs of ambulatory legs, and four spinous pads on the legs. The primary papillæ of the neotropical character with conical bases. Generative opening between the legs of the penultimate pair. Feet with only two papillæ.*

## **SUMMARY OF DISTRIBUTION.**

### **DISTRIBUTION OF THE SOUTH AFRICAN SPECIES—**

Slopes of Table Mountain, neighbourhood of Williamstown, Plettenberg Bay—Cape Colony.

## DISTRIBUTION OF THE AUSTRALASIAN SPECIES—

Queensland—Australia.

North and South Islands—New Zealand.

## ORIENTAL REGION—

Sumatra.

## DISTRIBUTION OF THE NEOTROPICAL SPECIES—

Nicaragua.

Valencia Lake, Caracas, Puerto Cabello, Laguayra, Colonia Towar—  
Venezuela.

Quito—Ecuador.

Maccasseema, Hoorubea Creek—Demerara.

Surinam (Peters).

Cayenne.

Santarem, Marajo at the mouth of the Amazon—Brazil.

Chili.

and in the following West Indian Islands—Cuba, Dominica, Porto Rico  
(Peters), Jamaica, St. Thomas, St. Vincent, Trinidad.

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EXPLANATION OF PLATES XXXIV, XXXV, XXXVI,  
XXXVII, XXXVIII, XXXIX, & XL,

Illustrating Mr. Adam Sedgwick's Monograph on the  
Species and Distribution of the Genus *Peripatus*  
(Guilding).

PLATE XXXIV.

*Peripatus capensis*, drawn from life. Life size. From a drawing by Mr. E. Wilson.

PLATE XXXV.

*Peripatus capensis*.  $\times 4$ . Dorsal view of a spirit specimen. From a drawing by Miss Balfour. This figure was originally published in vol. xxiii of this Journal.

PLATE XXXVI.

The figures on this Plate originally appeared in vol. xxiii of this Journal. They are from drawings by Miss Balfour.

FIG. 2.—A leg of *P. capensis*, ventral view.  $\times 30$ .

FIG. 3.—A right leg of *P. capensis*, viewed from the front side.

FIG. 4.—The last leg of a male specimen of *P. capensis*, ventral view to show the papilla, at the apex of which the accessory gland of the male, or enlarged crural gland, opens to the exterior.

FIG. 5.—Ventral view of head and oral region of *P. capensis*. -

PLATE XXXVII.

FIG. 6.—*P. Edwardsii*.  $\times 4$ . Dorsal view of a specimen with thirty-three legs. From a drawing by Miss Balfour.

FIG. 7.—*P. novæ-zealandiæ*.  $\times 4$ . Dorsal view. From a drawing by Miss Balfour.

FIG. 8.—*P. Moseleyi*.  $\times 4$ . Dorsal view. From a drawing by Miss Balfour.

FIG. 9.—Fourth leg of *P. Balfouri*. Ventral view. From a drawing by Mr. E. Wilson.

FIG. 10.—A piece of skin from the dorsal region of *P. Balfouri*. From a drawing by Mr. E. Wilson.

FIG. 11.—Terminal portion of fourth leg of *P. Edwardsii*. From a drawing by Mr. E. Wilson. (The colour of this figure is not that of the specimen.)

## PLATE XXXVIII.

All the figures on this Plate, except Fig. 16, are from drawings by Mr. Wilson. Fig 16 is from a drawing by Mr. Hill.

FIG. 12.—Leg of *Peripatus Edwardsii*. Ventral view.

FIG. 13.—Head of *P. Edwardsii*. Ventral view.

FIG. 14.—Portion of skin of one of the Copenhagen West Indian specimens, labelled *P. Edwardsii*.

FIG. 15.—Sixth left foot of *P. novæ-zealandiæ*. Front view.

FIG. 16.—Terminal part of antenna of *P. novæ-zealandiæ*.  $\times 120$ .

## PLATE XXXIX.

All the figures on this Plate, except Figs. 21 and 21a, are from drawings by Mr. W. H. Hill, executed under the supervision of Professor Moseley. Figs. 21 and 21a, by Mr. Wilson.

FIG. 17.—*P. novæ-zealandiæ*. A specimen of another colour. Dorsal view.  $\times 6$ .

FIG. 18.—Head of *P. novæ-zealandiæ*.  $\times 32$ . Dorsal view.

FIG. 19.—Portion of ventral surface of *P. novæ-zealandiæ*.  $\times 28$ .

FIG. 20.—Oral papilla of *P. novæ-zealandiæ*.  $\times 100$ .

FIG. 21.—Fourth leg of *P. novæ-zealandiæ*. Ventral view.

FIG. 21a.—Foot of the same fore-shortened, so as to show the dorso-median papilla.

## PLATE XL.

Figs. 22, 23, 24, 25, 26, from drawings by Mr. Wilson. Figs. 27 and 28, from drawings by Miss Balfour.

FIG. 22.—Ventral view of a posterior leg of *P. Edwardsii*.

FIG. 23.—Ventral view of hind end of *P. novæ-zealandiæ*.

FIG. 24.—Ventral view of hind end of *P. Balfouri*.

FIGS. 25 and 26.—Jaw blades of *P. Edwardsii*.

FIG. 25. Inner blade. The diastema is rather too marked.

FIG. 26. Outer blade.

FIGS. 27 and 28.—Jaw blades of *P. capensis*.

FIG. 27. Inner blade.

FIG. 28. Outer blade.

FIG. 29.—Skin of ventral portion of leg (close to the pads) of *P. Trinidadensis*, copied from Gaffron. The figure shows the form of the simple papillæ, and two of the composite papillæ of the row next the proximal pad.

FIG. 30.—Skin of leg of *P. novæ-zealandiæ*. From a drawing by Mr. Hill.



## Notes on the Anatomy of *Peripatus capensis* and *Peripatus Novæ-Zelandiæ*.

By

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THERE are a few anatomical details in which these two species of *Peripatus* differ both from one another and from *P. Edwardsii*, the anatomy of which has been described by Gaffron (2).

### CRURAL GLANDS.

I have examined several legs of *P. capensis*, both of males and females, and have found a crural gland in every one, except the first pair of legs.

Except those of the fourth and fifth, and in the male of the last pair of legs, the glands all resemble one another in their structure, in the position of the gland and duct, and in the point at which the latter opens, viz. on the ventral surface of the leg external to the opening of the duct of the segmental organ.

The glands of the fourth and fifth pairs of legs are very much smaller than the others, and open internally to the segmental organs, in the angle formed by the junction of the leg with the body. The gland of the last leg of the male is very long, and extends forwards through many segments of the body, being apparently modified in connection with the male generative organs.

These organs have all been previously described by Professor Balfour (1).



In none of the legs of *Peripatus novæ zealandiæ*, of which I examined sections, did I find any crural glands, either in the male or female. I took legs from the various parts of the body in both sexes, and in all cases the segmental organs were present, and the legs contained a much larger supply of muscles than those of *P. capensis*, but there were no traces of crural glands in any case, even in the last leg of the male.

In *P. Edwardsii* Gaffron (2) states that the crural glands are absent in the female, but are present in some of the segments of the male, there being in some of them two pairs.

#### SEGMENTAL ORGANS.

In *Peripatus novæ zealandiæ* the external aperture of the generative apparatus is placed on the ventral surface of the body in front of the last (fifteenth) pair of legs. In this pair of legs there are no segmental organs, so that the generative ducts are apparently the modified segmental organs of the last segment.

In *Peripatus capensis*, in which the generative aperture is situated at the posterior end of the body, immediately in front of the anus and behind the last pair of legs, segmental organs are present in the latter.

In *P. nova zealandiæ*, as was described in *P. capensis* by Professor Balfour (1), the segmental organs of the fourth and fifth pair of legs are much larger than the rest.

#### ACCESSORY GLANDS OF THE MALE.

In *P. capensis*, in addition to the enlarged crural glands of the last pair of legs, the male generative apparatus is provided with a pair of glandular tubes, which lie on each side, and dorsally to the ductus ejaculatorius, into which they open at the point where it opens to the exterior. These accessory glands were first mentioned by Professor Moseley (4),

and their position and mode of opening were described by Professor Balfour (1).

In *P. novæ zealandiæ* these accessory glandular tubes are also present, but their relations are somewhat different. They lie more laterally in the body. Each gland starts as a blindly-ending tube near the posterior end of the body, and passes forwards for a short distance. It then bends sharply on itself, and passes backwards to its external opening, which is situated near the posterior end of the body at its ventro-lateral angle, external to the nerve-cord. This position of their openings is clearly seen, both on dissection and in sections. Thus they open quite independently of the vas deferens, therein differing from those of *P. capensis*. They also differ from the accessory glands of *P. Edwardsii*, which Gaffron (2) describes as opening with the anus.

#### VAS DEFERENS.

To the naked eye the main difference between the vas deferens of *P. capensis* and that of *P. novæ zealandiæ* appears to be in their relative lengths, that of the former being much the shorter. This difference seems to be due to the very great difference between the spermatophores formed by the two species.

The vas deferens of *P. novæ zealandiæ* very closely resembles that described by Gaffron in *P. Edwardsii*. The whole of the posterior part of the duct is filled by an enormously long spermatophore, which is surrounded by a horny case. The internal cavity is enlarged in several places and in these regions is filled with spermatozoa, the external case being thin and composed of a single layer. In the remainder of the spermatophore the lumen is very small, and the case very thick and composed of several layers of horny substance. The whole spermatophore has, in fact, precisely the same structure as that described by Gaffron<sup>7</sup> in *P. Edwardsii*.

The structure of the walls of the vas deferens of *P. novæ zealandiæ* is also similar to that of *P. Edwardsii*, except

that the secretion globules are arranged in irregular masses in the cells near their ends, which abut upon the lumen, instead of having the regular arrangement described as occurring in the latter. The structure of the walls of the testes in *P. novæ zealandiæ* differs from that *P. Edwardsii*, in that in the latter Gaffron (2) states that there is no epithelial lining, whereas those of the former are lined by a layer of fairly deep columnar cells with large nuclei, their ends, which abut upon the lumen, being rounded. There is a layer of muscles external to the epithelium.

In *P. capensis* the spermatophores are small rounded bodies, enclosed in a thin, structureless case, and filled with spermatozoa.

In its lower part, where the vas deferens is filled with spermatophores, the cells lining it are somewhat flat, are much vacuolated, and stain very slightly. Just in front of the region where the fully formed spermatophores lie the cells are continued into small masses of unstained matter containing very deeply staining globules lying in the lumen of the duct. These masses probably form the cases of the spermatophores, and are secreted by the cells with which they are continuous. In front of this region the cells become columnar, the nuclei being closely packed at the bases of the cells. The cell protoplasm also stains very deeply. The spermatophores of *P. capensis*, after they have been shed, are easily seen by examining with a lens the dorsal surface of a female. They appear as small, round, whitish bodies, lying on the skin of the animal, and when teased are found to be filled with spermatozoa.

I have not had the good fortune to see a spermatophore of *P. novæ zealandiæ* after it has been shed, and I only assume that the horny case found in the vas deferens is a spermatophore, because Professor Moseley (4) and Gaffron (2) both describe it as such. But it is strange that it should differ so largely from *P. capensis* in this respect.

The ovarian funnel (receptaculum ovarum of Kennel (3)), described by Gaffron (2) in *P. Edwardsii* as lying on the ovi-

duct, between the ovary and the receptaculum seminis, is not present in *P. novæ zealandiæ*. The receptaculum seminis, with its two ducts, is present, and the oviduct in that region is much coiled and vesiculated.

These observations were made at the suggestion of Mr. Sedgwick, to whom I am indebted for providing me with the necessary material.

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**On the Construction and Purpose of the so-called  
Labyrinthine Apparatus of the Labyrinthic  
Fishes.**

By

**Doctor Nicholas Zograff,**  
of Moscow.

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With Plate XLI.

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IN the year 1797 two Dutch sailors, Daldorf and John, sent information to the Linnean Society of London as to the remarkable capacity of *Anabas scandens* to crawl from one pool of water into another, to climb up bushes and trees, to spend several days without water, &c., before the beginning of a dry season.<sup>1</sup> Since then almost every year one or the other journal or paper has given various travellers' accounts of the interesting life and habits of these fishes. Notwithstanding the variety of these accounts they all agree in one respect, viz. in trying to show that the Labyrinthici are remarkable for their highly-developed capacity of accommodation, and for their striking viability. Cuvier and Valenciennes, for example, in their natural history of fish, tell us how the *Anabus* can spend hot seasons in the slime of a dry water-basin (very much like the *Protopteri*), or how in the markets of the East Indies the *Ophiocephali* will keep on moving a long time after their insides have been cleaned out by the fishmongers. Besides that, we learn from the accounts of travellers that

<sup>1</sup> 'Transactions of the Linnean Society of London,' vol. iii, 1797.

these fishes develop more mental activity than any other species of the same class; such instances we see, for example, in their mode of nest building (*Macropodus*, *Trichogaster*), their changes of basins (*Anabas*, *Ophiocephalus*), and, lastly, in their way of getting food (*Toxotes*). Whilst communicating their observations on the life of *Labyrinthici*, travellers have not found it necessary to acquaint us with the anatomy of these fishes.

I have not found in existing literature any other reports on the inner construction (anatomy) of the *Labyrinthici* than those published in the important works of Cuvier and Valenciennes,<sup>1</sup> and in the work of Wilhelm Peters,<sup>2</sup> describing the gill-apparatus of some of the *Labyrinthici*. Both these authors took interest in that striking apparatus, which, thanks to its complicated exterior, received the name of "the labyrinthine apparatus."

It seems Cuvier was the first and probably the only author who examined the labyrinthine apparatus, Peters having been more interested in the relation between that apparatus and the skeleton of the clavicles. Cuvier thought this apparatus to be a complex of very thin bone lamellæ or plates, which served, sponge-like, to retain water for the purpose of moistening the gills of the fish when in the open air. These bone lamellæ, according to Cuvier, are nothing but projecting parts of the pharyngeal bones; their surface is covered with a great quantity of thin sanguiferous vessels, which apparently receive the blood from the general gill-artery. However, Cuvier says he is not quite convinced of that, having only had for his experiments samples kept in spirit, thus making it difficult to trace such thin vessels as the artery of the labyrinthine apparatus. Cuvier's views as to the construction and physiological importance of the apparatus have found credit in science, and there is not a good manual that does not describe it in the same manner as Cuvier did. As to

<sup>1</sup> 'Histoire naturelle des poissons par Cuvier et Valenciennes,' Paris, 1831, vol. vii, p. 328.

<sup>2</sup> Willh. Peters, "Ueber das Kiemengerüst der Labyrinthfische," 'Müller's Archiv für Anatomie und Physiologie,' 1853.

the work of Peters, this author tries to prove that the labyrinthine bones correspond not to the upper pharyngeal bones, which are merely the upper fourth segments of the hindmost branchial arches, but are strongly developed third segments of those branchial arches. Peters does not say a word about the construction of the soft parts of the labyrinths. Besides these two works I have not met with any other account of this interesting apparatus.

I have been able to make a detailed analysis of a labyrinthine apparatus of a *Macropodus* (*Polyacanthus venustus*, Cuv.). For my experiments I had little fishes brought up in my aquarium from the roe ejected by a female given to me by our indefatigable practical zoologist, A. S. Meschersky. Besides that (thanks to the kind permission of Professor Bogdenoff, the Director), I studied a specimen of *Anabas scandens*, var. *macrocephalus* and *Osphromenus olfax*, from the collections of the Moscow Zoological Museum.

All these fishes had the labyrinthine apparatus set inside the gill-operculum, and surrounded on all sides by a capsule, or walled with a thin membranous net. Its construction is the same as the lining of the cavity of the mouth; in it can be distinguished the epithelium of the surface, the connective tissue cutis, and scattered here and there pigmented cells. From the above we have the right to draw the conclusion that the sides or partitions of this capsule are only projecting cutaneous coverings of the inner surface of the gill-operculum. Indeed, if we examine under a moderate power the inner surface of a well-prepared gill-operculum of a *Macropodus*, we shall see on it a little narrow slit leading to the capsule of the labyrinthine apparatus, and connecting its cavities with the mouth and gill-cavities of the fish.

The same relation betwixt the gill-cover and the labyrinthine capsule exists in the other fishes which I have examined, viz. *Osphromenus olfax* and *Anabas scandens*.

The labyrinthine apparatus rises up into the cavity of the capsule from its inner side, which touches the exterior sides of the branchial arches (fig. 2). Notwithstanding Cuvier's



very accurate description of the exterior view of the labyrinthine apparatus in several species of the Labyrinthici, his description seems to be deficient in thorough acquaintance with the other sides of the apparatus, i. e. relative to dorsal, pectoral, front and back surfaces of the fish, the study of which is very important, as we shall see later, for the purpose of forming a just idea of the designation or purpose of that organ.

I shall begin with the apparatus of *Anabas*. Cuvier describes it as a complex of numerous very thin bone lamellæ lying over one another, and joined in the middle by a piece by which they are fastened to the branchial arches. The space between these lamellæ, according to Cuvier, is so small, as to enable them easily to detain water.

If we take an exterior view of the labyrinthine apparatus we can readily agree with what Cuvier has said about its construction and purpose; but, taking a profile view of the same (fig. 3), we are prone to suspect the truth of Cuvier's explanation. Indeed, the labyrinthine apparatus of *Anabas* does not consist of numerous laminae, but only of three<sup>1</sup> thin wavy lamellæ, one over the other, which become the larger the nearer they are to the point of fastening to the branchial arches; besides that the distance between each lamellæ is much wider than it seems to be when seen from above. Measured with a pair of compasses these distances or intervals were found to vary from 1.5 mm. to 2.75 mm. in breadth. We leave the reader to judge if an apparatus consisting of three lamellæ, of which the uppermost is 5 mm. long and 4 mm. broad, the middle one from 7 to 8 mm. broad, and the undermost 11 mm. long and 9 mm. wide, can detain much water. There are three spaces to detain water: one between the first and second lamellæ with a surface of about 15 square mm. and about 1.5 deep; another between the second and third lamellæ with a surface of about 60 square mm. and 2.5 mm. deep; a third one between the hard lamella and the sides of the pouch of the labyrinthical apparatus with a surface of about 80 square mm., and varying in depth according to wrinkles or

<sup>1</sup> After 'Günther's Manual of Ichthyology,' 3—5.

furrows formed here by the sides of the pouch. Experiments show that water is not detained in sufficient quantities between small plates with such a distance between them. I have tried to fasten together covering glasses in such a manner as to keep their sides parallel, with a distance from 1 to 3 mm. between each, and have found that with a surface of the glasses equal to 324 square mm., and with a distance of 1 mm. between each, the surface of water detained therein was equal to about 80 square mm.; with a distance of 2 mm. the surface of detained water was still less, and with a distance equal to 3 mm. the water was accumulated on a surface exceeding a little 0.5 mm. just round the cork that kept the glasses together. The quantity of water between the lamellæ was again still smaller if, instead of glasses, cartoon or British paper was used. Consequently the apparatus of Anabas, if applied for the purpose attributed to it by Cuvier, would in any case function imperfectly.

The apparatus of a *Macropodus* is still less fit to function in that way. It also consists of three parallel lamellæ or plates (see figure 4) which are placed in such a manner as to be quite unable to obtain water. The (first) top plate is so bent that its back part only remains parallel to the middle one; the third one forms a rectangle with it; the lower part is elongated more towards the pectoral surface of the fish, whereas two top lamellæ have grown in the opposite direction (see drawings 4 and 1).

The labyrinthine apparatus of *Osphromenus olfax* is so much like the apparatus of *Anabas*, that the aforesaid can be wholly applied to it.

But what are, then, properly the functions of the labyrinthine apparatus of the *Labyrinthici*?

A study of the fine microscopic structure of this organ gives us a right to make a supposition that will better explain its functions than the supposition made by the great naturalist.

The projecting bone of the third segment of the last branchial arch serves as support or basis to the labyrinthine apparatus (see Pl. XLI, fig. 8, *os.*).

This bone basis is very fine and consists of a typical (partly described by Kölliker)<sup>1</sup> bone tissue, in which star-like bone elements are not seen; when the section is made in a direction parallel with the surface of the lamellæ one can distinguish in the thickness of the bone ramous canals (described by Kostler), which make it look something like the dentine of teeth.

The bony basis is covered by a periosteum, which consists of very fine long and flat cells, and passes into a connecting adipose tissue, which, on its external surface, becomes a connective tissue (cutis); the cutis is covered by an epithelium; among the cells of this can be seen numerous goblet-like mucous cells.

From the above one sees that the labyrinthine apparatus is not a very complicated organ, and by its structure approaches the general typical structure of the skin coverings of fishes; but, as we shall see directly, special elements of the labyrinthine apparatus appear to be strongly modified.

Let us begin with the layer of connective tissue which lies next to the periosteum. This connective tissue consists of star-like cells with very long processes, and with a small cell-body and a little nucleus. These cellules, connected by their outshoots, form a netted tissue (fig. 8, *ctj. ad.*); between the meshes of this tissue are big, fat, adipose cells, that make a fresh tissue look very odd; but generally there remain no traces of fat in the sections, because the preliminary preparation in spirit, chloroform, &c., dissolves the fat.

It is only in objects prepared in osmic acid that the fat is retained where it is when sections are made (fig. 8); but meanwhile an organ without fat differs very much from one with it, as the fat in a tissue does not lie in mass, but in small round groups (*ejt. ad.*). The skin covering over these groups of fat is lifted or raised, whereas between them the coverings are much thinner, and consequently the surface of

<sup>1</sup> A. Kölliker, "Ueber verschiedene Typen in der microscopischen Structur des Skelettes der Knochenfische," 'Verhandlungen der physikalisch-medicinischer Gesellschaft zu Würzburg,' Band viii.

the labyrinthine apparatus under a microscope looks very much like a counterpane or a stitched soft lining with edged risings (fig. 10).

The meshes of the netting with fat in them get narrower and narrower the nearer they are to the cutis, and in the cutis the star-like connective tissue becomes fibrous. In this fibrous tissue over the groups of adipose cells one sees numerous capillary vessels (figs. 8 and 9, *cp.*), which form very pretty and characteristic braids or interweavings. These braids are in relation with the risings of the adipose masses or accumulations; between these accumulations capillaries are not observable. All the above-described accumulations or gatherings of adipose tissue have their separate arterial and venous branches; these branches rise to the surface of the accumulation, ramify severally, and partly pass into the capillary network of the cutis. Thus every part of the capillary network, with its separate adipose accumulation, has its special arterial and venous branches, and is connected with the nettings of other risings only by means of these branches. The capillary net of every rising has the form of a very pretty rosette (figs. 11, 12). This rose looks as if composed of separate petals, shaped out by the bendings of the meshes of the capillaries. The capillary windings of every petal are of three and seldom of four rows, wherefore the petal consists of an external, middle, and interior vessel. These vessels communicate on one side with the arterial branches, and on the other with the venous branch, so that in every petal can be observed an arterial and a venous half, or, to be more precise, one half that brings in the blood, and the other which lets it out from the interweavings.

The connective tissue that lies next to the cutis somewhat changes its appearance at the edges of the lamellæ of the labyrinthine apparatus. Here it is so swollen, and has such an appearance, that it can hardly be taken for a connective tissue (figs. 7 and 8, *cjt. mrg.*). Here it has no adipose matter; its cells become much thicker, more juicy, but their offshoots get so small that in sections they can be observed only when



the tissue has been split asunder into its component parts by means of fine needles, after it has been macerated for thirty-six hours in weak alcohol.

On its outside the cutis is covered with an epidermis of many layers (figs. 7, 8 and 9). This epidermis consists of numerous very small cells, scattered among which there is a quantity of mucous goblet-like cellules.

The latter are not seen in sections kept in alcohol and prepared in paraffine or soap, but they are well observed in sections prepared in osmic acid, and embedded in the white of egg according to the method of Kalberla. In such sections we observe that the number of goblet-like cells in the epidermis is very great, and that consequently these cellules can let out a considerable quantity of slime or mucus which covers the labyrinthine apparatus. The bottom of such cells is fast set in between other cells of the epidermis, and that is the reason why when teased they come out with irregular edges (fig. 3); one can observe in their goblet-like cavity a fine irregular protoplasm network and also a slime or mucus, the traces of which are seen outside the cell.

Having described the construction of this apparatus, so complicated and entangled externally, but so simple in its microscopic structure, I now return to its functions.

The first view of the strongly-developed capillary networks which are separated from the exterior by a fine epithelium of two or three layers and have arterial and venous vessels, and let only one or two corpuscles of blood through their cavities, makes us suppose that these capillary nets are the principal part of the organ. If, on the other hand, we remember that the organism of labyrinthine fishes must have adaptations for the characteristic, partly terrestrial or amphibious mode of life which is described by all authors, we shall have to seek in the organism of these fishes for such adaptations, and we must hope to meet with organs which will admit oxygen to the blood, not only from the air dissolved in water, but also from the atmosphere. The labyrinthine apparatus is such an organ. To establish a decisive view as to the physiological

functions of any organ would be possible either after exact or precise physiological experiments, or after having functionally studied the anatomy of the organ by comparing its structure with the structure of already well-known organs, the physiological functions of which are indisputable. The first method we cannot adopt. Notwithstanding my trying to introduce a very fine bent glass tube under the gill-operculum into the cavity of its labyrinthine pouch, it seemed impossible to do so without making ruptures through which little bladders of gas do not enter in the pipe but pass out. Perhaps if I had examined a greater amount of living material I could have accumulated and analysed a certain quantity of gas from the labyrinthine pouch, but the material I had was insufficient, and therefore I could not solve the question by mere experimenting. I then applied myself to the study of facts got by anatomy. Could the capillary net that has its arteries and veins be an organ for oxygenising blood? Did it let in venous blood and let out arterial, or vice versa? To solve the question I applied injections. Injections through the arteria branchialis, which is very fine and slender, gave no results; injections through the spinal aorta almost the same; I say "almost," because once after having made some unsuccessful injections I happened to inject some of the fluid through the aorta into the labyrinthine apparatus, and into a part of the branchial arches in a direction opposite to the course of the blood. But this not quite successful experiment, together with the results obtained on another occasion, convinced me that the labyrinthine apparatus is in reality a supplementary respiratory apparatus, helping the fish to breathe while in the open air or in the damp atmosphere of drying water-basins. The causes of my supposition are as follows:—Cuvier had made a supposition that the vessels of the labyrinthine apparatus are supplied with blood from the gill-artery which passes through a separate branch. But for all the preciseness of Cuvier's experiments this great naturalist did not succeed in seeing the supposed connection, and had to limit himself to supposition. All my efforts seemed to fail till I happened to fall upon a

very simple and convincing method. For long I took great pains to find a means of injecting one way or the other some fluid into the vessels conducting blood to the labyrinthine apparatus, but unfortunately I did not succeed. But two or three times I thought the fine light blue mass prepared according to Beal did penetrate through the gill-arteries from the heart into the apparatus, and that is the reason why in my remarks published in 1886 I ventured to say that Cuvier's hypothesis was very probable.<sup>1</sup>

Operating with chloroform upon *Macropodus* I observed that both the vessels of the labyrinthine apparatus and the gill-vessels of the fishes thus operated upon were overfilled with blood. Then I tried to rapidly curdle the blood by pouring some boiling water over the organ, and then making it hard with alcohol. My experiment proved to be successful. Not only the labyrinthine apparatus and the gill-vessels, but even the "bulbus arteriosus" were filled with coagulated blood, wherein one could very well distinguish the red corpuscles. After that I began to prepare sections of the part of *Macropodus* which lies next to the gills and its labyrinthine apparatus, and found that the blood with its red elements could be tinted with boracic carmine so as to enable one to discern the finest blood-vessels.

Several sections thus prepared convinced me that the artery leading to the labyrinthine apparatus (fig. 7, *ar. lb.*) is a branch of the artery of the fourth branchial arch (*ar. br.*), and consequently furnishes the apparatus with venous blood, the blood returning from the apparatus to the spinal aorta through the junction which I had already observed before, and through which the injected mass passed into the apparatus. So the labyrinthine apparatus is a supplementary apparatus of the fourth branchial arch, and the circulation of the blood of the gill-apparatus of *Labyrinthici* differs from the circulation of other *Teleostei* in the presence of an arterial branch (and

<sup>1</sup> "Ueber den sogenanntess Labyrinthapparat der Labyrinthfische (*Labyrinthici*)," von Nicolaus Zograff, 'Biologisches Centralblatt,' Band i, No. 22, 1886, p. 687.

probably of a vein too) from the fourth arch to the labyrinthine apparatus (fig. 13). In certain other fishes we meet with the same branches of gill-arteries. Johann Müller, in his famous work on Ganoid fishes, describes the artery of the undeveloped extra gill as an arterial branch of the first branchial arch.<sup>1</sup> Therefore, that the artery leads to the supplementary gill-apparatus from the gill-artery is not an anatomical rarity, but a consequence of the greater development of capillaries, and their particular disposition in the labyrinthine apparatus. If we remember that Peters proved the labyrinthine apparatus to be only a part of the branchial arch irregularly developed, we must, in my opinion, have expected that the labyrinthine apparatus would receive its artery from the artery of its arch, and that its function would be the same as that of the other branchial arch, but adapted to the special wants of these semi-terrestrial fishes.

<sup>1</sup> J. Müller, 'Ueber den Bau und die grenzen der Ganoiden und ueber das natürliche System der Fische,' Berlin, 1876.



## EXPLANATION OF PLATE XLI.

Illustrating Dr. Nicholas Zograff's paper "On the Construction and Purpose of the so-called Labyrinthine Apparatus of the Labyrinthic Fishes."

FIG. 1.—The labyrinthine apparatus of *Macropodus venustus* (from the side).  $\frac{4}{1}$ .

FIG. 2.—The labyrinthine apparatus of *Anabas scandens*, var. *macrocephalus* (Java) (from side).  $\frac{2}{1}$ .

FIG. 3.—The labyrinthine apparatus of *Macropodus* from behind. (Natural size.)

FIG. 4.—The labyrinthine apparatus of *Anabas* from behind. (Natural size.)

FIG. 5.—One of the calyciform cells of the epithelium of the labyrinthine apparatus (*Macropodus*).  $\frac{750}{1}$  (Leitz, homogen immers.  $\frac{1}{16}$ ).

FIG. 6.—A cell of the connective tissue of the labyrinthine apparatus (*Macropodus*).  $\frac{750}{1}$  (Leitz, hom. imm.  $\frac{1}{16}$ ).

FIG. 7.—Transverse section through the labyrinthine apparatus of *Macropodus*. *ar. br.* Arteria branchialis. *ar. lb.* Arteria apparati labyrinthiformis. *lb.* Apparatus labyrinthi. *ar. lb., vn. lb.* Arteria et vena appar. labyrinthi. *cjt. adp.* Conjunctiva adiposa. *cjt. mrg.* Conjunctiva marginalis. *ar. br.* Arteria arcus branchialis. *ep.* Epithelium.  $\frac{60}{1}$ , Hartnack,  $\frac{2}{3}$ .

FIG. 8.—Part of the transverse section through the labyrinth apparatus. *ep.* Epithelium. *cp.* Capillares labyrinthi. *cjt. mrg.* Conjunctiva marginalis. *cjt. ad.* Conjunctiva adiposa. *pg.* Pigmentum. *ct.* Cutis. *v. a.* Vasa arteriosa. *os.* Os apparati.  $\frac{180}{1}$ , Hartnack,  $\frac{2}{5}$ .

FIG. 9.—Part of a section through the apparatus, fixed with osmic acid. *ep.* Epithelium. *cl. gl.* Cellulæ glutinosæ. *ct.* Cutis. *cp.* Capillares. *ad.* Conjunctiva adiposa.  $\frac{235}{1}$ , Leitz,  $\frac{1}{8}$ .

FIG. 10.—Part of the surface of the labyrinthine apparatus. *c. ad.* Groups of adipose tissue. *a.* Arteriæ. *v.* Venæ.  $\frac{30}{1}$ , Hartnack,  $\frac{2}{3}$ .

FIG. 11.—Part of the rete mirabile of the apparatus.  $\frac{30}{1}$ , Hartnack,  $\frac{2}{4}$ .

FIG. 12.—Schematic figure of the rosette of the rete mirabile.

FIG. 13.—Schematic figure of the gill circulatory system of labyrinthic fishes. *cr.* Cor. *ao.* Aorta. *lb.* Apparatus labyrinthicus. *br.* Branchiæ. *a. br., v. br.* Arteriæ et venæ branchiales.

## Studies on the Comparative Anatomy of Sponges.

### I. On the Genera *Ridleia*, n. gen., and *Quasillina*, Norman.

By

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With Plate XLII.

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SOME months ago, when going over the large collection of Sponges in the British Museum, I came upon a curious little specimen,<sup>1</sup> which a cursory examination soon showed to be of exceptional interest. I was therefore led to make a careful investigation of the minute anatomy, and soon discovered that the specimen in question was the type of a new genus of Monaxonid Sponges allied to *Quasillina* on the one hand, and *Suberites* on the other. For purposes of comparison, I was further led to make as complete a re-examination as possible of the minute anatomy of *Quasillina*, which led to an almost complete confirmation of what Dr. Vosmaer has already published on the subject, and also to the discovery of some interesting new points.

As, therefore, the present paper treats of the anatomy of two distinct though closely allied genera, I have thought it desirable to divide it into two main parts. These two parts are, however, very intimately connected with one another, and perhaps the chief interest of the paper lies in the comparison

<sup>1</sup> Labelled, "H. M. S. 'Porcupine,' Station 82," and registered in the collection 83, 12, 13, 69.

of the two types and in the conclusions to be drawn therefrom. Hence I propose, at the end of the paper, to give a short summary in which the points of difference and of resemblance between the two genera will be pointed out and discussed.

Some of the sections were cut in the laboratory of the Zoological Society, at the Zoological Gardens, and others in the laboratory of the Royal School of Mines, South Kensington, and I have great pleasure in taking the present opportunity of expressing my thanks to the authorities of both these institutions, and especially to Professor G. B. Howes and Mr. Beddard, for the great facilities for work afforded to me.

With regard to the figures illustrating this paper, I feel that a few words of explanation are desirable. None of the figures, excepting those of mere external form and of spicules, are intended for exact representations of individual preparations. What I have been unable to make out in one section I have found in others, or vice versâ, and the figures are the result of the repeated examination of a large number of preparations. In drawing them, however, the camera has been largely used, and, although they are to a certain extent diagrammatic, I believe them to be far more instructive than any mere facsimile drawings of individual sections could be. Figure 7 is a pure diagram showing what I believe to be the arrangement of the canal system in *Ridleia oviformis*, after having repeatedly examined a large number of sections, both transverse and longitudinal.

In his report on the Hexactinellida of the "Challenger" Expedition,<sup>1</sup> Professor Schulze, who is undoubtedly the greatest living authority on the anatomy of Sponges, observes: "If I had attempted to copy the individual sections exactly as they appeared, the essential and typical could not, as a rule, have been distinguished from the unessential and accidental, except, of course, by giving a larger number of illustrations than seemed justifiable for such a slight possible advantage," and with this I most heartily agree.

<sup>1</sup> P. 4.

I. The Genus *Ridleia*, n. gen.

This genus, which I wish to dedicate to my friend and late colleague, the Rev. S. O. Ridley, who is so well known for his work on Sponges, may be diagnosed as follows:

“Sponge corticate, with a highly-developed system of fibrous tissue. Consisting of a single solid body terminating above in an osculum which leads into a well-defined oscular tube with fibrous walls. Spicules monactinal, styli or tylostyli, confined almost entirely to the ectosome. Skeleton composed chiefly of stout longitudinal bands of spicules situate in the inner portion of the ectosome, and of tufts of small spicules projecting at the surface of the Sponge. Canal system canalicular, flagellated chambers diplodal.”

A generic diagnosis based upon a single species, especially when only a single specimen is present, must be more or less tentative, and very possibly future investigations upon fresh material will lead to a modification of the above.

*Ridleia oviformis*, n. sp.

External Characters.—The single specimen in the collection (fig. 1) consists of an egg-shaped body terminating above in a slight papilla upon which lies the small osculum, and thinning out below into a flattened peduncle. The peduncle appears, from the existence of certain flattened surfaces (*aa*), to have been attached to pebbles during life, in a manner similar to that which occurs in *Quasillina* (fig. 8).

The specimen is 15 mm. in height and 7 mm. in greatest breadth. It has a very compact, cork-like consistence, and its colour in spirit is pale yellow.

The osculum (figs. 1 and 2, *o*) is single, very minute, and situate on a small papilla at the summit of the Sponge.

Arrangement of the Skeleton.—The skeleton is almost entirely confined to the ectosome, or that outer portion of the Sponge in which there are no flagellated chambers. Its most important constituent is a ring of stout, longitudinally dis-



posed bundles of large spicules (fig. 3, *l. sp.*), situate in the inner portion of the ectosome. Outside of these comes a broad zone of irregularly interlacing, separate, large spicules, which occupy the greater portion of the ectosome, and which give support to the numerous bundles or tufts of small spicules (fig. 3, *sp. b.*) which project outwards at the surface of the Sponge. The only remaining portion of the skeleton is a zone of somewhat obliquely disposed and not very well-defined bundles of small spicules (fig. 3, *i. sp.*) occurring in the outermost portion of the choanosome. These bundles are separated from the well-defined longitudinal bundles occurring in the inner portion of the ectosome by the two layers of fibrous tissue, which I shall describe later on. The remainder of the choanosome appears to be entirely free from spicules, a fact which is probably to be accounted for by its dense, cork-like consistence rendering their presence unnecessary.

The Spicules.—The spicules are all tylostyli of various sizes, each consisting of a long, straight, or slightly curved, cylindrical shaft, terminating at the base in a subglobular head, and at the apex in a fine point. They are of two chief sizes. The larger ones (figs. 4 and 5) are straight, or nearly so, and measure up to about 0.9 mm. in length, with a diameter in the thickest portion of the shaft of about 0.014 mm. The small spicules (fig. 6), which are almost confined to the surface brushes and to the innermost zone of longitudinal bundles, differ somewhat in shape from the large ones. They are very slender, frequently somewhat curved, and they taper very gradually to almost imperceptible fineness at the apex. They measure about 0.2 mm. in length by 0.002 mm. in maximum diameter of the shaft.

The Ectosome.—In describing the ectosome and choanosome, I shall, of course, leave out of account the spicular elements, which have been more conveniently treated of apart.

The ectosome (fig. 3, *ect.*) is composed for the most part of a transparent, gelatinous-looking tissue, containing ill-defined fibres and other mesodermal cells. Towards the outside it becomes more granular and stains more deeply, and no doubt

it is limited externally by an epithelium of flattened cells, which, however, I have not made out in my sections. The most remarkable character about it, however, is the presence, in its innermost portion, of two well-developed layers of fibrous tissue. In the outer layer (fig. 3, *l. f.*) the fibres are arranged longitudinally, and in the inner layer (fig. 3, *c. f.*) horizontally or circularly. The outermost layer is not perfectly continuous, but is occasionally interrupted by strands of fibres given off towards the outside of the Sponge from the inner layer. In short, the outer fibrous layer consists of bundles of densely packed, longitudinally disposed fibres, wedged in between the inner fibrous layer and the stout longitudinal skeleton-bundles described above (fig. 3, *l. sp.*). The inner layer is about 0.024 mm. thick, and is composed of densely packed, circularly arranged fibres, giving off, as already described, occasional outgrowths towards the circumference. At intervals one can distinctly make out much elongated, granular nuclei. In parts there are distinct traces of a second layer of longitudinal fibres internal to the layer of circular fibres. The histological characters of the different layers appear to be thoroughly identical. The individual fibres are capable of separation from one another, and are then seen to be very slender and greatly elongated. They are, I believe, identical with the myocytes of Sollas,<sup>1</sup> and I attribute to them a contractile function.

While speaking of the fibrous tissue, I may also notice that the central oscular tube of the Sponge (fig. 2) is encased in a thick sheath of fibrous tissue, continuous in the neighbourhood of the osculum, with the true ectosomal layer. Here, again, we distinguish between two chief layers of fibres, circular and longitudinal. The circular fibres occur on the inside, i.e. next to the lumen of the tube, and the longitudinal on the outside. Fibrous tissue also occurs to a greater or less extent in connection with the main branches of the canal system.

The Choanosome. — The term choanosome has been applied by Sollas, in his 'Preliminary Report on the Tetrac-

<sup>1</sup> Article "Sponges," in 'Encyclopædia Britannica,' ed. ix, p. 419, fig. 21, *e.*

tinellida of the "Challenger" Expedition,<sup>1</sup> to that internal portion of the Sponge body which contains the flagellated chambers, as distinguished from the ectosome, in which, it will be remembered, there are no flagellated chambers at all.

In *Ridleia oviformis* the choanosome (fig. 3, *ch.*) is almost entirely filled up by the closely-packed flagellated chambers which are embedded in a very sparingly developed granular ground-substance, in which it is difficult to make out any cellular constituents. A remarkable character in the choanosome, and to a certain extent in the ectosome also, of the specimen under description, is the occurrence of great numbers of minute, highly refringent, yellowish granules, which, from the fact that they occasionally exhibit a moniliform arrangement, I believe to be bacteria of some description. They are especially abundantly developed around the flagellated chambers, and around the inhalant and exhalant canaliculi. They occur both in stained and unstained preparations, and I am inclined to believe that they were present in the living Sponge.

The fibrous tissue surrounding the various parts of the canal system has already been described in connection with the similar tissue in the ectosome.

The Canal System.—The canal system is characterised by its canalicular character, or, in other words, by the absence of irregular lacunæ, such as exist in *Halichondrine* Sponges. The pores (fig. 3, *p.*) are minute, and scattered apparently without order and rather sparsely over the general surface of the Sponge. They may be seen in sections leading into the narrow, elongated subdermal cavities, which penetrate the various layers of the ectosome and terminate in slightly expanded spaces (subcortical crypts of Sollas) beneath the layer of circular fibres. These subcortical crypts, one of which is shown in fig. 3, are the only portions of the canal system which can be considered as at all lacunar. From them the inhalant canaliculi, leading sooner or later to the flagellated chambers, take their origin.

<sup>1</sup> 'Sci. Proc. Roy. Dub. Soc.,' vol. v, pt. vi, p. 177.

The flagellated chambers are more or less elongated or pear-shaped sacs, measuring about 0.05 mm. in length by 0.03 mm. in transverse diameter. They are provided with narrow excurrent and incurrent canaliculi as represented in the diagram, fig. 7. The canaliculi are extremely difficult to make out, but I have repeatedly examined a large number of sections, both transverse and longitudinal, and have satisfied myself of their existence. Their lumina, possibly owing to the contraction of the Sponge in spirit, are especially obscure, being only very occasionally discernible. They commonly appear as short, slender cords, leading to the proximal or distal end of the chamber, as the case may be, and are chiefly visible owing to the presence around them of the minute refringent granules already referred to. As usual in ordinary spirit specimens little can be made out concerning the collared cells. They appear to be very minute, and all I have succeeded in observing are their small nuclei and a number of irregular, gelatinous-looking processes projecting into the lumen of the chamber, and probably representing the remains of the flagella. The exhalant canaliculi unite together and open ultimately into the central oscular tube, whence the stream of water is discharged through the single osculum at the summit of the Sponge (fig. 2, *o.*).

I have endeavoured to represent in fig. 7, in a purely diagrammatic form, what I believe to be the relations of the flagellated chambers to the exhalant and inhalant canaliculi. It thus appears that the flagellated chambers are of the type described by Sollas as "diplodal," although the inhalant canaliculi appear to be but short. It is worthy of note that I have seen in one instance a flagellated chamber apparently opening direct out of a subcortical crypt without the intermediation of a canaliculus. It is obvious that such an occurrence would be most likely to take place, if anywhere, where the canal system is lacunar, and, as already pointed out, the subcortical crypts are the only portions of the canal system in *Ridleia oviformis* which are lacunar.



II. The Genus *Quasillina*, Norman.

The only species of this genus as yet described is Bowerbank's *Quasillina* (*Polymastia*) *brevis*, a common Shetland form, living in moderately deep water. As the somewhat complicated history and synonymy of this Sponge have lately been fully treated of by various authors,<sup>1</sup> I need not enter into the question here, but will proceed at once to the description of its general form and minute anatomy.

*Quasillina brevis*, Bowerbank sp.

**External Characters.**—Externally the Sponge is seen to consist of a usually somewhat flattened, oval body, perched on the summit of a short stalk (fig. 8). At its lower extremity the stalk is somewhat expanded, and the expanded portion is generally attached to a small pebble. At its upper extremity the body terminates in a slight mammiform prominence, at the summit of which there is a single minute osculum (figs. 8 and 9, *o.*).

The osculum is usually so much contracted and so difficult to make out that its existence has, until quite recently, been a matter of some doubt; and Vosmaer,<sup>2</sup> who has given by far the most complete account of the genus yet published, observes that he "never saw an opening at the top larger than those where the sea-water enters." Ridley and Dendy<sup>3</sup> have, however, demonstrated that an osculum is, at any rate sometimes, present, and my recent researches on the arrangement of the canal system in the body of the Sponge justify us in assuming that there is always one, although it is frequently found more or less completely closed up in preserved specimens.

According to Vosmaer (*loc. cit.*) the general shape of the

<sup>1</sup> Vide Ridley and Dendy, 'Report on the Monaxonida of the "Challenger" Expedition,' p. 225.

<sup>2</sup> 'Sponges of the "Willem Barents" Expedition, 1880-81,' p. 20.

<sup>3</sup> 'Report on the Monaxonida of the "Challenger" Expedition,' p. 226, woodcut, fig. 10.

Sponge is subject to considerable variation, but such strongly marked deviations from the ordinary type as he figures have not come under my notice, and I believe the essential characters remain fairly constant.

Certain rectangular marking on the surfaces of the Sponge, due to the arrangement of the skeleton in the ectosome, are very characteristic; their nature will be best understood by reference to fig. 8.

One of the most obvious of the characters of the species is the general flaccidity and emptiness of the body. Thus, Bowerbank<sup>1</sup> remarks, "When divided longitudinally the parietes of the Sponge did not exceed in the dried state the fourth of a line in thickness at any part, and the internal cavity extended the whole length of the Sponge. The greater number of them were more or less in a compressed state, but in some there were strong indications that this was due rather to collapse than to natural form," and Norman<sup>2</sup> begins his diagnosis of the genus with the words "Sponge consisting of a single clavate hollow body." I lay especial stress upon this character as it will be found later on to be very intimately connected with the arrangement of the canal system, and is one of those characters in which the two genera, *Ridleia* and *Quasilina*, differ very markedly from one another. I may forestall my account of the canal system so far as to state that the hollow condition insisted upon by Bowerbank and Norman is chiefly a post-mortem character, due to the shrinkage of the loose and delicate choanosome.

A full-grown specimen is usually less than an inch in height, and less than half an inch in greatest width. Fig. 8 represents the Sponge of the natural size.

Arrangement of the Skeleton.—This portion of my subject has already been more or less fully treated of by Bowerbank, Norman, and Vosmaer (loc. citt.), and, as I have but little to add, I may dismiss it briefly.

<sup>1</sup> 'Mon. Brit. Spong.,' vol. ii, p. 64.

<sup>2</sup> "Last Report on Dredging among the Shetland Isles," 'Brit. Assoc. Rep. for 1868,' p. 329.

By far the larger and most important portion of the skeleton lies within the ectosome. It may be best studied by cutting out a portion of the body wall (ectosome) and examining it as a transparent object with a low power of the microscope. A number of stout longitudinal bands or bundles of large spicules radiate upwards from the peduncle to the osculum, more or less parallel with one another, but sometimes branching. These bundles occur in the innermost portion of the ectosome. They support on their outer surfaces a layer of large, transversely, or obliquely disposed spicules arranged in rather confused and irregular bands. The spicules of both these systems are more or less parallel with the surface of the Sponge, but we now come to a third system of spicules placed at right angles to the surface of the Sponge, and consequently at right angles also to the other spicules. This third system consists of innumerable tufts or brushes of small spicules (fig. 9, *sp. b.*), whose apices project from the surface of the Sponge, and whose bases rest upon the spicule bands of the second system. These tufts are placed at a little distance from one another, and, when viewed from the surface, are seen to be arranged in a somewhat reticulate manner, so as to leave certain irregular spaces free from their presence. Within the choanosome the skeleton is very feebly developed, but is not so poorly represented as in *Ridleia*. It consists chiefly of separate bundles of small stylote spicules, each bundle (fig. 11) being composed of a number of spicules arranged parallel to one another. These structures closely resemble, on an enlarged scale, the well-known "trichite bundles" or "trichodragmata" of some Halichondrine Sponges (e. g. *Esperella Murrayi*), and I attribute to them the same function as has been attributed to the trichodragmata by Mr. Ridley and myself. In our report on the Monaxonida of the "Challenger" Expedition we suggest that these last serve, like straw in mortar, to bind together the soft, gelatinous tissue in which they lie. The trichodragmata are, of course, bundles of microsclera or flesh spicules; the occurrence of similar isolated bundles of megasclera has not, I believe, hitherto been noted. As they are

composed of styli the term "stylodragmata" might be applied to them. The presence of the stylodragmata in *Quasillina*, while they are absent in *Ridleia*, is probably to be attributed to the much less compact character and consequently greater need of support of the choanosome in the former Sponge.

**The Spicules.**—The spicules are nearly all styli (i. e. monactinal spicules simply rounded off at the base and pointed at the apex), but occasionally the base is swollen into a head, when the spicule becomes tylostylote.

They are, as already indicated, of two chief kinds.

(1) Large, straight, or slightly curved, fusiform styli, usually gradually sharp-pointed at the apex and narrowing considerably towards the base. These measure up to about 0.9 mm. in length, with a maximum diameter of 0.0144 mm.

(2) Small, slightly curved styli, very gradually sharp-pointed at the apex, but not so markedly fusiform as the large ones. These spicules are all of pretty much the same length, viz. about 0.24 mm., but the variation in thickness is very remarkable. Both stout and slender ones occur mixed up promiscuously in the surface tufts, the stout ones measuring about 0.0096 mm. in diameter, and the slender ones only about 0.002 mm. The two sizes appear to keep fairly distinct from one another, and one cannot help being struck by the general absence of intermediate stages. The stouter ones appear much more distinctly fusiform than the slender ones.

**The Ectosome.**—The ectosome consists of a somewhat granular but jelly-like matrix, with small, nucleated, multipolar cells embedded in it. It stains more deeply towards the outside, and on the extreme outside I have detected what appear to be traces of a single layer of flattened epithelial cells. This epithelium appears also to line the subdermal cavities in the ectosome. Fibrous tissue appears to be entirely absent, at any rate in most parts.

Here, however, we are met with a considerable difficulty in deciding the exact limits of the ectosome. In the wall of the oscular tube there is a very well-developed system of fibrous tissue, which seems hitherto to have entirely escaped observa-



tion, and as the wall of the oscular tube, at any rate in its upper portion, seems to me to have as much claim to be regarded as ectosome as it has to be regarded as choanosome, I shall describe it in this place. The osculum (fig. 9, *o.*) leads direct into a widely-expanded canal, the oscular tube, about 0.8 mm. in diameter. The walls of this canal present a series of well-defined circular ridges of fibrous tissue. Owing to the fact that the oscular tube does not run parallel with the plane of section, the section figured shows these fibrous ridges (fig. 9, *f. r.*) in transverse section in the upper portion of the tube, and in vertical longitudinal section in the lower portion. The ridges themselves do not necessarily run parallel with one another but may branch and anastomose. Each consists, for the most part, of a dense band of slender fibres (fig. 12) running round the oscular tube, and showing here and there elongated granular bodies, which I believe to be nuclei. The fibres themselves exhibit a very distinct, wavy outline, strongly calling to mind the appearance of ordinary white fibrous connective tissue. This fibrous band is covered on the outside by a layer of curious, granular, flocculent-looking tissue, the nature of which I do not at present understand (fig. 12, *f.*). I have little doubt that these rings of fibrous tissue around the oscular tube act as sphincter muscles, whereby the diameter of the tube is regulated. The concentration of the fibrous tissue in distinct annular bands is probably to be regarded as indicating a higher degree of differentiation than that which occurs in *Ridleia*, where the fibrous tissue forms a continuous sheath.

The Choanosome.—Owing to the lacunar character of the canal system the choanosome is much less dense and compact than in *Ridleia*. The amount of mesodermal tissue in proportion to the rest of the choanosome is also greater, and it exhibits numerous deeply staining, irregularly shaped cells (probably the amœboid cells) embedded in a coarsely granular and at the same time somewhat gelatinous-looking matrix (fig. 10, *m. c.*).

The Canal System.—We owe by far the greater portion of our knowledge of the arrangement of the canal system in

this Sponge to the researches of Dr. Vosmaer (*loc. cit. supra*), and I am able to do little more than confirm the results which he has arrived at.

As already stated, the canal system is lacunar. The scattered pores (fig. 9, *p.*) lead into expanded subdermal cavities (*s. c.*) lying between the tufts of spicules in the ectosome. These in turn communicate with a system of more or less lacunar inhalant channels in the choanosome. The inhalant lacunæ are separated from the exhalant lacunæ by strands of mesodermal tissue in which the flagellated chambers are embedded (fig. 10, *f. c.*). Many flagellated chambers communicate directly with one and the same inhalant or exhalant lacuna, but occasionally I have seen traces of what appear to be short and rather wide canaliculi (fig. 10, *a*). These would seem to be developed when the situation of the chamber prevents it from opening immediately into a wide canal or lacuna.

The chambers themselves are usually somewhat elongated, but their actual shape is a good deal affected by the state of contraction of the tissues. Good-sized examples measure about 0.045 mm. in length and 0.02 mm. in transverse diameter.

The exhalant channels open into branches of the oscular tube, whence the water is discharged through the osculum.

Thus it would appear that the canal system of *Quasillina* belongs essentially, as stated by Vosmaer, to his third type, while that of *Ridleia* belongs to his fourth type. I believe, however, that the canalicular and non-calicular types of canal system cannot be sharply defined from one another, and that they will be found to pass by insensible gradations into one another.

### General Conclusions.

The genera *Ridleia* and *Quasillina* are shown by their spiculation, skeleton arrangement, and general form to be closely allied, and it is not until we have examined properly prepared stained sections that we are able satisfactorily to

comprehend the points of distinction between them. We then see that they differ to such an extent in their minute anatomy that we cannot include them both in the same genus.

From the foregoing description it appears that the first exhibits the canalicular and the second the lacunar type of canal system; in *Ridleia* the inhalant and exhalant channels are canalicular, and the flagellated chambers are provided with special inhalant and exhalant canaliculi, while in *Quasillina* the inhalant and exhalant channels are for the most part lacunar, and the flagellated chambers open directly into them without the intermediation of narrow canaliculi. At the same time there is some evidence to show that these two types of canal system cannot be sharply defined from one another, and that flagellated chambers with, and others without special canaliculi may coexist in the same Sponge.

It is noteworthy that in *Quasillina* the chambers, although usually opening directly into the lacunæ of the canal system, are elongated in form like those of *Ridleia*, and not, as in the *Halichondrina*, where such a mode of opening is typical, spherical, or subspherical.

Both genera are remarkable for the development of the fibrous tissue. In *Ridleia* it is largely developed in the ectosome proper, and in the wall of the oscular tube, being arranged in well-defined layers of longitudinal and circular fibres. In *Quasillina*, on the other hand, it is almost entirely absent from the ectosome proper, but is well developed in the wall of the oscular tube, where it forms definite annular ridges in which the close-packed fibres (myocytes) have a distinct, wavy outline.

The mode of occurrence of the fibrous tissue in this and in other genera in which it occurs, indicates that its function is a contractile one, or, in other words, that the fibres are muscular fibres. The annular bands of fibres around the oscular tube of *Quasillina* are probably to be regarded as sphincter muscles.

The genus *Quasillina* has been recognised for a long time as a member of the sub-family *Suberitidæ*. It is, however,

a very aberrant one, and the new genus *Ridleia* forms a connecting link between it and the other members of its sub-family.

Probably *Quasillina* is to be regarded as a more highly modified form than *Ridleia*. I have already pointed out that the arrangement of the fibrous tissue in definite bands indicates a higher degree of modification than that which exists in *Ridleia*, where it forms more or less continuous sheaths, and the occurrence of the stylodragmata appears to me to be an adaptive modification resulting from the lacunar character of the canal system, and the general delicacy of the choanosome. Stylodragmata occur, so far as I am aware, in no other members of the group.

Professor Schulze, in his 'Report on the "Challenger" Hexactinellida,' and elsewhere, has expressed the opinion that the polyactinal type of spicule is the primitive form from which the monactinal type has been derived by abortion of the rays. Although in a previous paper<sup>1</sup> I upheld, for reasons therein given, the contrary hypothesis, I am now inclined to regard Professor Schulze's view as the more correct one.

It is, I believe, generally admitted that the swollen base, or head, of a typical Suberitid spicule, together with the corresponding enlargement of the axial thread, indicates the position where other rays were at one time united with that one which now alone remains. In the typical Suberitidæ, then, and in *Ridleia*, all rays but one have disappeared, but their former presence is still indicated by the head of the tylostylote spicules. In *Quasillina* the spicules are still more modified, and even the head has, in most cases, disappeared.

Judging, then, from the condition of the fibrous tissue and of the spicules, we should expect the canal system of *Quasillina* to be less primitive than that of *Ridleia*, and, in general, the lacunar type of canal system, as it occurs in the Monaxonida, with chambers opening directly into wide

<sup>1</sup> Dendy and Ridley, "On *Proteleia Sollasi*," 'Ann. and Mag. Nat. Hist.,' ser. 5, vol. xviii, p. 153.



lacunæ, to be less primitive than the canalicular type, in which the chambers are provided with special canaliculi. There is not sufficient evidence at present to show whether or not this is the case, but I think it not impossible that it may be so.

## EXPLANATION OF PLATE XLII.

Illustrating Mr. A. Dendy's paper "Studies on the Comparative Anatomy of Sponges. I. On the Genera *Ridleia*, n. gen., and *Quasillina*, Norman."

FIGS. 1—7.—*Ridleia oviformis*.

Fig. 1. Entire Sponge,  $\times 2$ . *o*. Osculum. *aa*. Flattened surfaces, by which the Sponge has probably been attached to pebbles.

Fig. 2. Longitudinal section, taken at right angles to the surface shown in Fig. 1,  $\times 5$ . *o*. Osculum, leading into oscular tube; the black line indicates the distribution of the fibrous tissue. (The figure is rather diagrammatic; the canals radiating towards the centre are exaggerated.)

Fig. 3. Portion of transverse section,  $\times 44$ . *ect*. Ectosome. *ch*. choanosome. *p*. Pore, leading into slit-like subdermal cavity. *e. c.* Exhalant canals converging towards the centre of the Sponge. *l. f.* Layer of longitudinal fibres cut across. *c. f.* Layer of circular fibres. *sp. b.* Bundles of small spicules projecting at surface. *l. sp.* Longitudinal bundles of spicules cut across. *i. sp.* Oblique fibres of spicules within the choanosome cut across. (A little diagrammatic.)

Figs. 4 and 5. Two of the larger tylostyli  $\times 190$ .

Fig. 6. One of the small tylostyli  $\times 500$ .

Fig. 7. Diagram of diplodal canalicular canal system, as it occurs in *Ridleia oviformis*,  $\times 190$ . *i. c.* Inhalant canal, giving off narrow canaliculi to *f. c.*, the flagellated chambers, which communicate again by narrow canaliculi with *e. c.*, an exhalant canal.

FIGS. 8—12.—*Quasillina brevis*.

Fig. 8. Entire Sponge attached to a pebble, nat. size. (After Ridley and Dendy, 'Report on the "Challenger" Monaxonida.') *o*. Osculum.

Fig. 9. Part of longitudinal section passing through the osculum,  $\times 23$ . *o*. Osculum. *p*. Pores. *s. c.* Subdermal cavities. *l*. Lacunæ of canal

system. *f. r.* Fibrous ridges on wall of oscular tube. *sp. b.* Bundles of spicules projecting at surface. (Rather diagrammatic.)

Fig. 10. Part of transverse section through choanosome,  $\times 190$ , showing arrangement of flagellated chambers and inhalant and exhalant lacunæ. *f. c.* Flagellated chambers. *l. l'.* Lacunæ of canal system. *m. c.* Mesodermal cells, probably amœboid. At *a* there is an indication of a canaliculus at one end of a flagellated chamber. (Rather diagrammatic.)

Fig. 11. Separate bundle of small styli (stylodragma) from choanosome,  $\times 284$ .

Fig. 12. Portion of a branched fibrous ridge from inner surface of wall of oscular tube, seen in section taken parallel to the wall of the oscular tube,  $\times 284$ . *n.* Elongated nuclei. *f.* Flocculent granular tissue covering the ridge.

(The spicules, except where separately figured, are represented in blue.)



## Kleinenberg on the Development of Lopadorhynchus.

By

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the University.

It is now more than a year since Professor Kleinenberg published, in the 'Zeitschrift für Wissenschaftliche Zoologie,' a long account of the development of a polychæte Annelid, *Lopadorhynchus*. Whether it is because of the extreme length of the paper, which extends over 225 pages, that the work has not attracted the attention it deserves, or because the very numerous illustrations include no diagrams, but are invariably exact drawings of the sections studied by the author, and require to be laboriously re-interpreted by the reader, or because the facts and views expressed are so novel and so much opposed to all preconceived notions of what mesoblast ought to be, the fact remains that this paper is little known by English readers.

The morphological importance of the questions raised by Kleinenberg concerning the origin of the mesoblast is so great, that a reproduction of those parts of his paper which deal especially with this subject calls for no excuse.

In an introductory chapter, the consideration of which I shall defer until the facts of the development of *Lopadorhynchus* have been presented to the reader, the author lays down the proposition that there is no such thing as a mesoblast as a specially differentiated germ layer. The existence of two primary germ layers in the Cœlomata, ectoderm and endoderm, homologous with the similarly-named layers in Cœlen-



terates, is admitted; the existence of a mesoderm, if by it we understand a tissue or aggregate of tissues interposed between the two primary germ layers, is not denied, but it is specifically denied that those intermediate tissues originate from a separate embryonic layer, composed of undifferentiated cells. Ectoderm and endoderm, says the author, are the foundations of all other tissues and organs, with the sole apparent exception of the germinal cells, not only in *Cœlenterata* but in all *Metazoa*. Tissues and organs originating directly from these layers take over with them the power of giving origin to other tissues and organs on their own account; in no part of the living body is the capacity for change entirely lost. By this the genetic relationship between any organ and the primary germ layers is not destroyed, it is only made more remote by the intercalation of one or more intermediate developmental phases. Say that an organ or tissue which originates directly from one of the primary germ layers is a primary tissue; it gives rise to other tissues which are secondary, those give rise to another series of tertiary tissues, and so forth. The mesoblast, so called, is in fact nothing more than the aggregate of these primary, secondary, and tertiary tissues, the precise origin of which is often obscured by the tendency to precocious development.

Let us see how this view is supported by the facts of the development of a single form. The account of the developmental phases of *Lopadorhynchus* is so long that it would be impossible to give details of the whole organogeny of the animal in the space of a short essay. I will therefore confine myself to a short description of the general development of the Annelid from the larval form, and will give the details of the formation of a few selected tissues and organs which have a special bearing on the question in hand.

The earlier developmental history of *Lopadorhynchus* was not studied; the youngest larva described is a true trochosphere, with a preoral ring of cilia, called by Kleinenberg by the convenient name of prototroch, dividing the body into preoral and oral lobes of nearly equal size. The stomodæum

marks the ventral surface, and is not yet connected with the archenteron. The latter is a closed sac, occupying the whole of the interior of the trochosphere, except that a pair of small slits on either side of the stomodæal invagination represent the remnants of the segmentation cavity. Both ectoderm and endoderm are composed of a single layer of cells. The ectoderm cells are colourless, their nuclei are distinct, but the cell outlines are difficult to see, and their size and shape vary in different parts of the larva. Those ectoderm cells which bear the cilia of the prototroch are, for instance, much larger than those on the oral and preoral lobes. The endoderm cells are coloured, and their inner ends are stuffed with yolk-granules. Two differentiations can be seen in the ectoderm of the aboral lobe (umbrella, Kl.). On the ventral surface, further removed from the aboral pole than from the prototroch, is a pair of arcæ, where the ectoderm cells are more closely packed together than elsewhere. These are the foundations<sup>1</sup> of the sense-plates of the head. A pair of thickened ectoderm arcæ can also be seen on the ventral sides of the oral lobe (sub-umbrella, Kl.), the foundations of the ventral plates, and close beneath the stomodæum an unpaired thickening of the ectoderm, forming a transient larval organ known as the ventral shield. The further important changes in the larva concern the fate of the ventral plates, and the appearance of the foundations of a number of organs on the preoral lobe. On the preoral lobe appear two pairs of prominences in front of the sense-plates, which are presently put into connection with the latter, and the three pairs of structures form a semicircle enclosing a field of thickened ectoderm, the head shield, which occupies nearly the whole ventral surface of the preoral lobe. A single symmetrical pit also makes its appearance towards the aboral pole. At a later period the sense-plates divide to form the foundations of the second pair of permanent antennæ anteriorly, and the foundations of the olfactory organs poste-

<sup>1</sup> I use the term "foundations" as the equivalent of the German word *Anlage*, which cannot be exactly translated into our language. The use of the term "rudiment" in this sense is clearly open to objection.

riorly. The second of the two pairs of prominences above mentioned is the foundation of the first pair of permanent antennæ.

In the oral field the ventral plates increase greatly in size, extend anteriorly and posteriorly, and become divided by a number of clear transverse lines into segments, but as yet there are no external furrows marking off one segment from another. Usually as many as eight segments make their appearance at once, and the number increases up to sixteen, but is very inconstant. In the next stage the number of segments is not added to, but each segment grows greatly in size, and soon the hinder part of the ventral plate begins to project beyond the oral lobe of the larva. Already in each segment a median, and a distal prominence, have made their appearance on each side of the body. These are the foundations of the dorsal and ventral cirrhi of the parapodia, and before long a third prominence appears between each pair of cirrhus-foundations, which is the foundation of the chætopodium. In further growth the vermiform segmented body of the Annelid, derived from the ventral plates, becomes more and more important, and preponderates over the oral lobe of the larva. The chætopodial elements grow out into the parapodia of the adult, and in so doing carry with them the dorsal and ventral cirrhi which, at first separate from the chætopodia, are eventually carried on the ends of the latter. At this stage the pre-oral lobe and the prototroch retain their primitive characteristics, and the larva has a broad, dome-like trochosphere head, with a vermiform body bearing parapodia. The foundations of the two pairs of antennæ have, however, grown out into processes projecting from the ventral surface of the pre-oral field, and the olfactory pits are developed as deep sacs, with a narrow, slit-like opening, which can be evaginated and drawn in again.

The final changes consist in the atrophy of the preoral lobe, the loss of the ciliated ring, the further growth of the two pairs of antennæ, and the completion of the parapodia with their setæ, &c.

The internal organs of the adult Annelid are developed by

successive differentiation of derivatives of the two primary layers, ectoderm and endoderm.

In the first place it may be stated that the adult *Lopadorhynchus* has no blood-vascular system, and Kleinenberg was unable to find its nephridia. The youngest larva observed had a well-developed provisional nervous system, consisting of a ring of nerve-fibres lying beneath the prototroch, and a series of ganglion-cells, connected by fine processes with the sub-prototrochal nerve-ring. It is unnecessary to enter into the exact arrangement of these ganglion-cells: they lie in the ectoderm of the preoral lobe of which they are differentiations, and although the cephalic ganglion of the adult animal and the sense-organs in connection with them are developed from the ectoderm of the preoral lobe, the central nervous system of the trochosphere has but very little share in their establishment. The whole of the nervous structures of the head of the adult are formed from three centres: firstly, from nerve ganglion-cells, which make their appearance at an early stage in the ectoderm of the preoral lobe; secondly, from parts of the sense-plates already mentioned; thirdly, from indifferent ectoderm cells. The more anterior of the two pairs of prominences, which have been described as appearing on the ventral surface of the preoral lobe, and are called by Kleinenberg the pole antennæ (*Scheitelantennen*), prove to be nothing more than cell-proliferations, and eventually form the anterior lobes of the cephalic ganglion of the adult. The remainder of the ganglion is formed from ganglion-cells and nerve-fibres which arise in connection with the sensory organs of the head (the two pairs of antennæ, the olfactory pits, &c.), to which are added cells derived independently from the ectoderm. The newly-formed cephalic ganglion is first placed in connection with the sub-prototrochal nerve-ring by means of commissural fibres; the angles of these commissures are afterwards produced posteriorly into the oral lobe, and, becoming subsequently connected with the anterior ganglion-pair of the ventral chain, form the periesophageal connectives. In a later stage of growth the cephalic ganglion retires from the



ectoderm, and lies in the cavity of the head, separated by a wide space from the head wall, except at its anterior end, where it retains its connection with the ectoderm. In the young larva there is no special nervous apparatus in the oral lobe, but the foundation of the ventral ganglionic chain can be detected in the ectodermic thickenings already described as the ventral plates. At an early period of development special nervous elements are found ventrad of the inner edges of the ventral plates, but lying outside of them; they are the first foundation of the central nerve-chain of the body. In connection with them rise small bundles of sense-hairs, arranged metamerically. Just beneath these sense-hairs is a mass of large nuclei, derived from the continued multiplication of the ectoderm cells of that region. They lie close upon the endoderm. The inner boundary of the ectoderm layer is quite distinct, but at a later period it disappears suddenly; at this point the endoderm becomes somewhat bent in towards the archenteron, so that a space is formed between it and the ectoderm. Many of the cells, proliferated from the ectoderm in the manner just described, find their way into this space. One might say that the ectoderm bursts through at this point, emptying its contents as an abscess might, between the previously existing cell layers (see Fig. 1).

As the result of this process there are established three layers—an ectoderm, a middle layer derived from it, and an endoderm. This division of the ventral plate is only complete in its anterior position, posteriorly it remains undivided. The middle layer gives rise to muscular tissue only, and hence is called muscle-plate; the external plate, or ectoderm of the ventral plate, may be called the neural plate. It gives rise to the ventral ganglion-chain, sense-organs, and also to non-nervous structures, the sacs of the setæ. These seta-sacs are formed by a proliferation of the cells of the anterior parts of the neural plates; they grow inwards as pear-shaped projections, and enter the muscle-plates. In the lateral parts of each neural plate is next developed the dorsal cirrus as a proliferation of cells, and a little later a similar proliferation, close to

the seta-sac, gives rise to the ventral cirrus. At a later stage the neural plates of the opposite sides of the body become connected together by a series of transverse commissures. These commissures are developed coincidently with the elonga-

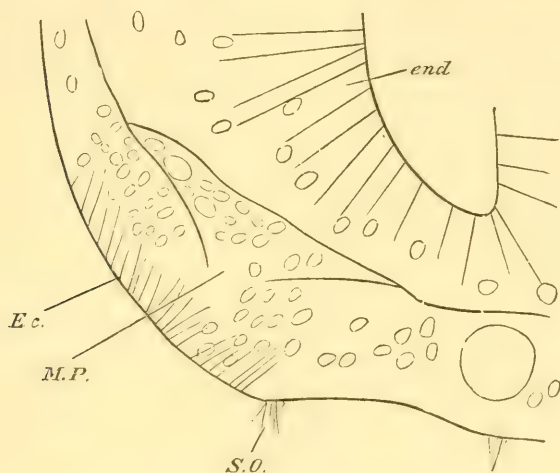


FIG. 1.—Transverse section of a young larva of *Lopadorhynchus*, showing the formation of the muscle-plate from the ectoderm. *Ec.* Ectoderm. *end.* Endoderm. *M.P.* Muscle-plate. *S.O.* Sense organ.

tion of the body in such a way that for each pair of seta-sacs a single commissure is developed. Each pair of seta-sacs with its transverse commissure represents a single somite. In addition to the transverse commissures, longitudinal fibres are developed towards the median edges of each neural plate; these put the ganglionic centres of the ventral chain into communication with one another, and form the longitudinal connectives. From their mode of formation the connectives are necessarily paired structures; subsequently they become intimately united together; but their paired structure is always distinguishable. At first both commissures and connectives lie directly upon the ectoderm, but subsequently become separated from it. The foundations of the dorsal and ventral cirrhi are divided into proximal and distal portions. The latter form bundles of

nerve-fibres communicating with the ventral nerve-chain. As the seta-sac grows in size the dorsal cirrhus is pushed further and further away from the ventral cord, so that the nerve connecting the two becomes longer.

Before the development of the cirrhi has progressed very far the segmentation has begun, not as a simple process of division of mesoblastic plates into somites, but by the differentiation of the already existing foundations of various organs. The tissues composing the muscular and neural plates are at first dense and homogeneous throughout, but now they become divided into masses of denser tissue, separated by transverse tracts of loose tissue, which mark the boundaries of the segments. Each segment of the neural plate contains the two halves of a rudiment of a ventral ganglion, two pairs of cirrhi, and a pair of seta-sacs, in addition to which are several masses of undifferentiated cells. The more anterior segments are further advanced than those posteriorly situated. The segmentation involves only the lateral moieties of the neural plates, it does not extend to the middle line. The ventral ganglion-chain is not, in fact, divided up into segments at any period of its development; and, although at a later stage the ganglia correspond exactly with the body segments, this does not alter the fact that the foundations of the organ, as well as the fully-developed chain of ganglia and connectives, are at all times continuous throughout the length of the body. A parapodial nerve system is developed, not directly from the ventral nerve-cord, but in connection with it; and the latter may be said to determine its formation.

The visceral nerve system of the adult is developed directly from the anterior ganglion pair of the ventral nerve-chain, by the differentiation and separation of its dorsal moiety. The cells thus separated spread over the pharynx, and in the earlier stages of development do not extend over more than the pharyngeal, and therefore ectodermal portion of the alimentary canal.

The muscular system, like the nervous system, is developed as separate larval and adult elements. The two arise

independently, and very little of the larval musculature passes over to the adult. The larval muscles originate from two ectoderm thickenings situated beneath the prototroch. Finally, the larva is provided with a muscular layer, which is to be found nearly everywhere between the ectoderm and endoderm. The exact arrangement of the larval muscles need not detain us: it only remains to be noticed that no part of the larval musculature is formed from the ventral plate, whereas the adult muscles are derived, if not entirely, for the most part from that structure. The separation of the muscle-plate from the neural plate has already been described: it must be borne in mind that both owe their origin to an ectodermal cell-proliferation. The muscle-plates grow rapidly in size and importance, partly through the addition of wandering cells derived from the ectoderm. The muscle-plates become segmented from before backwards, so that each somite has a pair of muscle-plates, which are separate from one another in the mid-ventral line. A seta-sac projects into the muscle-plate on either side of each segment, dividing it into four regions—an anterior, a posterior, a median, and a lateral region. The ventral muscles of the adult are derived from the median region, the dorsal muscles from the lateral region, the parapodial muscles from the anterior and posterior regions. (See Fig. 2.) In the cavities of the parapodia in the adult are found peculiar stellate muscle-cells, which have no connection with the ventral plate, although they appear to be remnants of the larval nervous system, they are far more probably derived from separate centres determined by the muscle foundations of the body.

The muscle-plate does not split into splanchnopleure and somatopleure in *Lopadorhynchus*, nor does this happen in many other Annelids (*Asterope*, *Nauphanta*, and others), but the musculature of the gut is formed by the aggregation of a number of single free wandering cells, derived originally from the ectoderm through the intervention of the muscle-plate. Thus we learn that the cœlom of the adult Annelid is neither an enterocœle nor a schizocœle, but is an archicœle, i. e. the



remnant of the primary body cavity existing between ectoderm and endoderm. The muscles of the head of *Lopadorhynchus* are derived from the body muscles, as is the case in *Polygordius* and other Annelids.

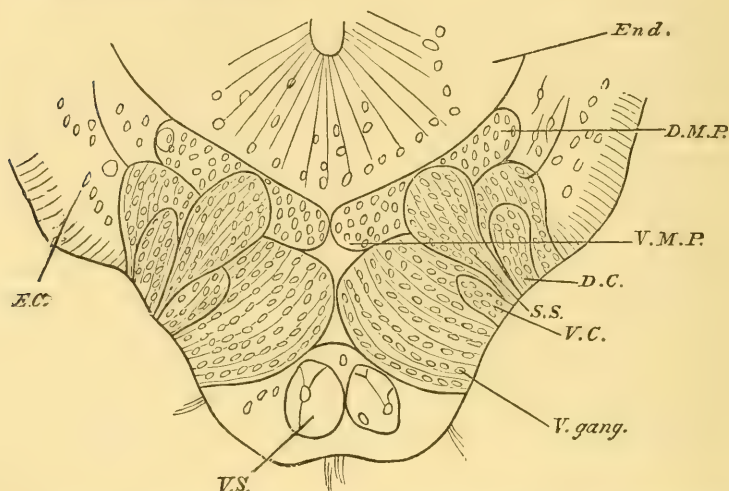


FIG. 2.—Transverse section of an older larva, showing the further development of the muscle-plates and the origin of the ventral ganglion chain, cirrhi, and seta-sacs. *E.C.* Ectoderm. *End.* Endoderm. *D.M.P.* Dorsal muscle-plate. *V.M.P.* Ventral muscle-plate. *D.C.* Dorsal cirrus. *V.C.* Ventral cirrus. *S.S.* Seta-sac. *V.gang.* Ventral ganglion. *V.S.* Ventral shield.

The seta-sacs are invaginations of the ectoderm, solid at first, but subsequently developing a lumen, the cells lining which secrete the setæ. The sac of the aciculum is formed as a special outgrowth of the seta-sac, which becomes partially constricted off.

The gonads of *Lopadorhynchus* are derived from the ectoderm. Earlier or later in development the ectoderm cells lying behind and to the side of the parapodial ganglia proliferate, and the mass of cells thus formed is invaginated in the form of a pear-shaped body projecting inwards towards the body cavity. In the female, cells are separated from the inner ends of these ingrowths, which develop into ova, wander free

in the body cavity, and settle anywhere on its walls. In the male, masses of cells are shed off into the body cavity, which become spermatoblasts.

There remains to be described the development of the pharynx and œsophageal glands of the adult. The stomodæum of the larva does not become the pharynx, but the latter is derived from a pair of gland-like stomodæal outgrowths, which subsequently fuse together and form the pharynx. The œsophageal glands are formed as three outgrowths—two lateral, one median and dorsal, from the pharynx.

The important facts which are to be gathered from the foregoing account are these: *Lopadorhynchus* has no mesoblast in the sense of a germ layer composed of undifferentiated cells. The larva has its own nervous system and its own musculature, no parts of either of which pass over to the adult, but are replaced by a new nervous system and musculature, and are afterwards aborted. The central nervous system of the adult is formed from a number of separate centres or foundations, the situation of which is in part determined by the pre-existing nerve centres of the larva, although the latter have no direct share in their formation, but act only as foci, in connection with which fresh groups of nervous elements are differentiated.

The muscular system of the adult is derived wholly from the ventral plates, as is also the whole ventral chain of ganglia, with its connectives and commissures. These ventral plates are, in their earlier stages, nothing more than thickenings of the ordinary ectoderm, the cells of which become subsequently divided into muscle-plates and neural plates. The muscle-plates give rise to the whole of the muscular system, both of the body walls, and of the gut; but they do not split into two layers, comparable to somatopleure and splanchnopleure, the cœlom being formed simply as an extension of the space existing between ectoderm and endoderm, the peritoneal walls of which are formed by cells derived from the muscle-plates. The neural plates give rise to the whole of the ventral ganglion chain, and besides this to other and different organs, viz. the

cirrhi, parapodia, and seta-sacs. All the tissues usually classed as mesoblastic are derived from the ectoderm; the endoderm appears to form nothing more than the lining of the gut.

The generalisations which Kleinenberg would found upon these facts may be briefly stated as follows:

New organs and tissues are always developed in connection with and through the intervention of pre-existing organs and tissues. That this must be true in a phylogenetic sense is obvious on reflection, for a new form with newly specialised organs must always be developed from a form in which the same vital functions were performed, less efficiently it may be, by other or less perfect organs. Hence, if ontogeny is a recapitulation of phylogeny it must also be true in an ontogenetic sense, but the fact has been overlooked because authors have been too ready to refer developing organs to the undifferentiated cells of the two primary layers, ectoderm and endoderm, or to a mesoblast, falsely assumed to be an undifferentiated third germ layer, homodynamous with the two first named.

In the Cœlenterata the two primary germ layers are present, and form all the tissues of the adult: each of them may give rise to differentiated tissues or organs, to which special functions are appropriate. Among the first tissues to be formed are the nervous and muscular, and since irritability and contractility are complementary to one another, these two tissues are invariably developed in such close connection that they may be said to be mutually determinant. But they are not structures developed *de novo*; they are the result of the specialisation of function of already existing cells, whether of ectoderm or of endoderm, and very frequently arise from the direct transformation of those cells. In the higher Metazoa such tissues derived from the primary ectoderm or endoderm because of the increased functional activity due to their specialisation, give rise to modifications in adjoining cells; these group themselves round the tissues first formed, and, becoming themselves specialised, lead to the formation of other tissues and organs. In some instances the cells newly formed are

joined to those already present to form a mass, the component units of which, although unlike, subserve the performance of some one physiological function (e.g. glandular and pavement epithelia, connective tissue, muscle-fibres); the whole aggregate forms a single organ, and the new differentiations only serve to increase its efficiency. In other instances groups of cells, subserving a special function, will induce changes in adjoining cells, which changes are the first step towards the establishment of new tissues and organs. In every case change of function is the guiding principle in the formation of fresh tissues and organs.

It is a mistake to suppose that a new organ is formed by the gradual growth and change of a pre-existing organ. Since Darwin showed that species through gradual modification are transformed into new species, it has been generally believed that organs similarly may go through slow series of uninterrupted modifications, the final result of which is the transformation of that organ into some other organ having an analogous though not wholly similar function, or even into some wholly different organ with entirely different functions. The phylogenetic and ontogenetic changes of the gill-slits in the Vertebrata are familiar instances of this supposed progressive modification of a single organ. As a matter of fact this process of direct change has seldom, if ever, taken place. In animals of simple organisation tissues and organs are formed to which special functions are appropriate. Their functional activity is, as it were, a disturbing element in the organism; it induces changes in neighbouring tissues, and gives the signal for new specialisations in them. The functional activities of the newly specialised tissues must always bear some relation to the function of the organ which determined their origin, and must either support or modify their action. The newly-formed tissues again affect the organism, their importance increases, and they may in their turn give rise to fresh tissues. Finally, they may become so important that they outweigh in functional importance the organ to which their origin was due; they then take its place, and the latter dwindles till finally it may disappear



altogether. This process, which is of the greatest importance, is called by Kleinenberg the development of organs by substitution. The organs resulting from the changes are the organs of substitution; those through which the changes are effected are the intermediary organs. In no case of substitution are the intermediate steps represented by an indifferent germ layer, but always by a functional and specifically differentiated organ.

One of the most striking instances of substitution is the development of the axial skeleton of the Chordata. Both phylogenetically and ontogenetically the transformation of an already existent specialised portion of the gut leads to the formation of a supporting skeletal rod,—the notochord. When once this is established it induces correlative changes in the muscles, which act more efficiently because of the firmer support. The muscular changes react upon the supporting rod, which no longer affords a suitable point d'appui for them, and is replaced by, not converted into, a segmented cartilaginous column. The very segmentation is caused by the muscles, for the cartilage is primitively unsegmented. Finally, the cartilage is inefficient, and is replaced by bone. It is most important to observe that each organ is functional and complete in itself for a time, and does not form any part of the organ which subsequently replaces it, but is entirely or very nearly aborted. The disappearance of the notochord is an excellent example, but many others could be given, all equally good—for instance, the successive development of pronephros, mesonephros, and metanephros.

The author claims that the theory of the development of organs for substitution gives an entirely new significance to the persistence of rudimentary organs. That organs which have had no functional importance should persist through long series of generations is surprising and inexplicable by conventional views. But if once it is recognised that they are intermediary organs their use in ontogeny becomes apparent. Phylogenetically they induced the formation of the organs which replaced them, therefore they are retained in order that, in ontogeny, they may give the impulse to the formation of those new organs of sub-

stitution, having done which they may either disappear (gill-slits of Vertebrates as such), or remain as obviously rudimentary structures.

The above considerations must lead to an entire remodification of the conventional assumption of a mesoblast. There is nothing in morphology about which there is so much disagreement as the homology of the mesoblast and the cavities included in it. The most diverse origins have been assigned to this supposed germ-layer; it arises from the outer germ-layer alone, from the inner germ-layer alone, from both together, from neither, from two special blastomeres, from every part of the living blastoderm (Sarasin), not from the blastoderm at all, but from the yolk (His). With so many contradictions before one, it is at least a step in advance when we can strike out on a fresh line, and begin a new series of observations on the assumption that there is no mesoblast. Whether Kleinenberg's views will stand the test of further proof is of course an open question, but it cannot be doubted that investigations undertaken from his point of view must be fertile of results. To trace back organs through the intermediary organs which gave them origin, and to establish homologies between the latter and the permanent organs of lower forms, is a task which offers many advantages to the researcher, and is likely to yield much surer and more satisfactory results than the attempt to refer an organ merely to one of the three primary germ-layers.

It must not be forgotten that the homologies of the mesoblast and cœlom are two of the most debateable questions in morphology. But, as Kleinenberg says, a hole is a hole the world over,—if we can establish the homologies of the walls bounding a cavity, there is no need to quarrel about the empty space itself. Already one can see the possibilities of satisfactory explanations, through the theory of substitution, of the cœlomic cavities of Arthropods, the greater part of which is shown by Sedgwick to be turgid blood-vascular space, and the various stages of cœlosis in the Hirudinea. Kleinenberg states that the cœlom of *Lopadorhynchus* is what would be conven-

tionally called an archicœle, i. e. it is derived from the original segmentation cavity, as is the cavity of the head in all Annelids. It is possible that this statement may be extended to all other Annelids in which the cœlom is stated to result from the splitting of the mesoblast into somatopleure and splanchnopleure, but against the probability of this view must be set the careful researches of Hatschek.

Finally, it is gratifying to find that Kleinenberg has insisted upon the intimate connection between morphology and physiology. Enough has been said in the foregoing pages to show how strongly he insists upon the dependence of function upon form. In the introductory chapter he condemns the theory of the Hertwigs, that the origin of cells can be predicated by their form, and shows from numerous examples that the form of cells is caused solely by their function and the mechanical necessities of their position. Naturally the two formative conditions, position and function, generally coincide; but if there is a contention between those conditions, function prevails.

In an abstract which has to be confined within certain limits of space, I am unable to give more than the most meagre outline of Prof. Kleinenberg's argument. It is enough, however, if I have succeeded in calling attention to his remarkable work, and in inducing morphologists to read carefully the formidable paper in which his results are published.

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